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LATENT LEARNING OBSERVED THROUGH NEGATIVE TRANSFER[1]

738 lg.

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The purpose of this study was to test for latent learning in the Blodgett-type situation by shifting, at the time of introduction of reward, one of the previously unrewarded groups of animals to a different maze. If there is latent learning in the no-reward period, negative transfer should occur in the shifted group, and a measure of latent learning should be the difference in errors between the shifted and unshifted groups, rather than the rate of error reduction in the unshifted group according to the usual procedure.

THE MAIN EXPERIMENT

Method

Subjects

The subjects were 70 naive, hooded rats, approximately 90 days old. Thirty-eight females and 32 males were distributed fairly evenly among seven groups. They were handled daily so that they were thoroughly tame at the beginning of training. One week prior to this time their feeding schedule was established. For 1 hr. each subject was placed singly in a feeding cage where more water and dog chow were present than it could consume. For the rest of the day it was kept with one to four others in a living cage where water was present all the time.

Apparatus

The apparatus consisted of two six-unit mazes, one of which was the mirror image of the other as shown in Figure 1. The walls and curtains were 5 in. high and painted gray. The baffles at the end of the blind alleys were painted white on one side and black on the other. In maze A the black sides, and in maze B the white sides, faced the blinds, and the opposite colors faced the approach to the exit from a particular unit. The goal boxes were white for maze A and black for maze B. Two sets of these boxes were used. The set which was used during the no-reward period never contained food. By moving the baffles to the opposite side, and by interchanging the right and left halves of the maze and also the goal boxes, one floor plan could be changed to its mirror image. (In a preliminary experiment, which is not reported here, we obtained evidence of negative transfer when hunger-food motivated rats were first trained in one maze and then shifted to the other maze.) The maze was not nailed to the floor but stood on a large brown piece of battleship linoleum on which it was shifted to a different location from trial to trial in order to eliminate tracking and facilitate cleaning.

General Method of Maze Training

After the feeding schedule had been established, and about 22 hr. after the last feeding, the animal was placed in the starting box. After 10 sec. the door was opened and the animal was allowed to proceed to the goal box. Whenever the subject entered a new unit of the maze and made a choice, the sliding door behind it was closed. The total time from start to goal was taken, and each entry into a blind alley was noted. The criterion for an error was pushing the curtain aside and facing the bend in the blind. Each day there were five runs, after which the animal was detained for 1 hr. in a carrying cage before being placed in the feeding cage. Reward in the goal box consisted of chewing at a large pellet of dog chow for 1 min.

Experimental Design

The design of the experiment followed in general the one originally used by Blodgett (1). There were seven groups of ten animals, and in each group five animals started in maze A and five in B. There was one control group which was rewarded from the beginning. The unrewarded animals were divided into six groups, two being rewarded on the second day, two on the third, and two on the fourth. They will be referred to as the 1-day, 2-day, and 3-day groups according to the number of days preceding the introduction of reward.

The important innovation was the shifting of one-half of the animals to the second maze when reward was introduced, while the other half continued in the same maze. It was expected that those 1-day, 2-day, and 3-day groups which were shifted to the other maze on the first day of reward would show negative transfer, whereas each of the three comparable groups which continued in the same maze on that day would show the often observed sharp drop of errors. We shall refer to the two sets of groups as the shifted and unshifted ones.

Table 1*A* presents a survey of the entire experimental design.

Training was continued until a criterion of three successive, errorless trials was reached.

Group Matching

The matching of groups during the no-reward periods was achieved by assigning the first two-thirds of the subjects at random to the different groups and the last one-third in such a way that the mean error scores

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[1] The authors wish to thank the Council on Research and Creative Activity of the University of Colorado whose financial support made this study possible.

were equalized. The result of this matching procedure was that the means of errors on the first nonrewarded day ranged from 17.9 to 18.5 for six groups, on the second day from 15.9 to 16.3 for four groups, and on the third day from 13.2 to 13.6 for two groups, as shown in Table 1*A*.

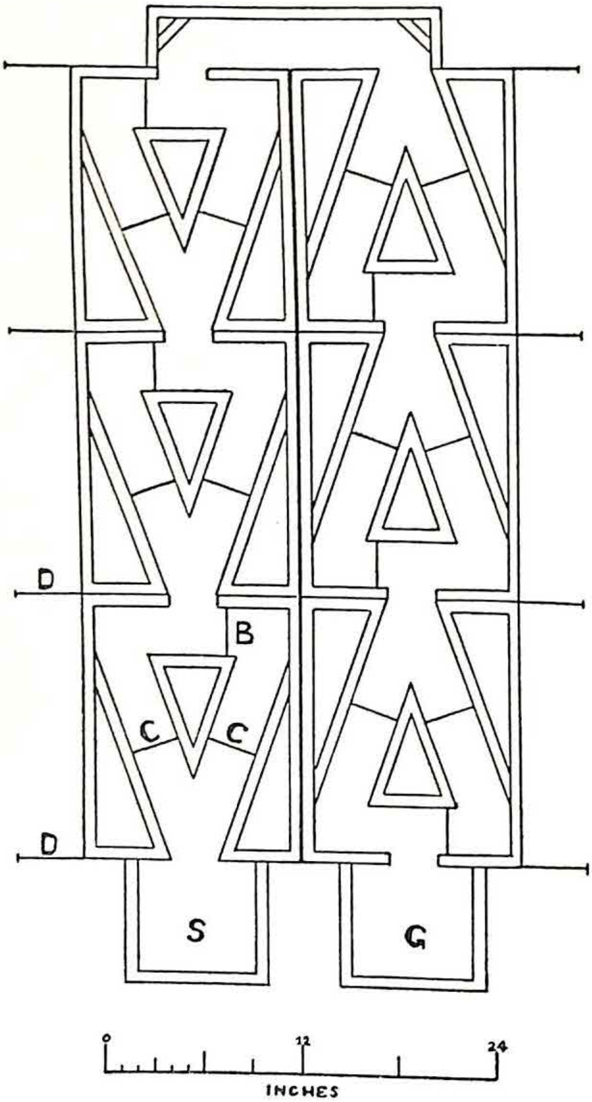

FIG. 1. Floor plan of maze A. In the first unit the curtains are indicated by *C*, the baffle by *B*, and the sliding doors by *D*. *S* and *G* indicate the starting and goal boxes.

The floor plan of maze B is the mirror image of maze A.

Results

In general the results in terms of errors present the following picture. The decline of errors in the control group was marked and steady from the start. The 1-day, 2-day, and 3-day groups which were continued in the same maze showed a slight decline during each of the three no-reward periods, followed by a sharp reduction of errors as soon as food was introduced. The three comparable groups which were shifted to a different maze did not behave uniformly. Contrary to expectation, the 1-day and 2-day shifted groups were like the comparable unshifted ones. It was only the 3-day shifted group that behaved as predicted by showing definite interference on the fourth day when the maze was shifted at the same time that reward was introduced. The details of this picture are presented in Tables 1 and 2 in terms of four separate measures, all involving errors.

The *first measure*, which needs some justification, consists of the mean errors per subject per day of four trials only instead of five. The first trial of the day is omitted in order to make the daily records more directly comparable. The first trial on the first day of the reward period cannot really be counted as a "rewarded" run inasmuch as there was no food expectation.

In all *unshifted* groups we find the typical sharp drop in errors from the last day of no reward to the day of introduction of reward (Tables 1*A* and 2*A*). The first two days of the 1-day group may also be compared with those of the 2-day group. On their first day in the maze their records are the same by matching. On their second day of training the rewarded 1-day group made 11.6 errors, and the unrewarded 2-day group 16.3, which represents a significant difference at the .02 level (Table 2*C*). A similar comparison can be made on the third day of training between the 2-day and 3-day groups.

Contrary to expectation, there was also a significant drop of errors from the unrewarded to the rewarded days in the 1-day and 2-day *shifted* groups (.001 and .01 levels), whose records were practically the same as those of the unshifted groups: There was no interference through running in a different maze under these conditions.

It was in the 3-day shifted group that interference was evident. The drop of errors when the maze was changed and reward was introduced was slight and insignificant as compared with the sharp drop in the unshifted group. There was a significant difference between the shifted and unshifted groups (.02 level) in contrast to the absence of similar differences in the 1-day and 2-day groups (Table 2*B*).

The *second measure* consists of the means of errors per subject on the last single trial of the no-reward period and the first single trial on the following day when food was introduced. It must be remembered that on this first trial no food expectation existed although food had been placed in the goal box. Table 1*B-a* shows a consistent error reduction for all groups except the 3-day shifted groups.

TABLE 1

A. Means of Errors per Subject per Day of Four Trials

CONDITION	CONTROL	1-DAY GROUPS		2-DAY GROUPS		3-DAY GROUPS	
No Reward						17.9	17.9
				18.0	17.9	16.3	15.9
		18.4	18.5	16.3	15.9	13.2	13.6
Maze Reward		same	shifted	same	shifted	same	shifted
	11.9	11.6	11.3	9.9	10.6	8.0	12.2
	9.5	8.9	10.6	8.3	9.0	6.3	9.7

B. Errors on the Last Trial Before and First Trial with Reward*

a. Mean errors per subject:							
Before reward		4.6	5.3	4.1	3.9	3.0	3.3
With reward*		3.4	3.9	3.3	2.7	2.7	4.2
b. Number of subjects whose errors:							
Increased		1	1	2	3	2	7
Remained the same		1	3	1	2	2	1
Decreased		8	6	7	5	6	2
c. No. of blinds entered:							
Before reward		3.7	3.6	3.5	2.7	2.7	2.8
With reward*		3.1	2.8	3.1	2.4	1.8	3.7
New on this trial		1.0	1.0	0.9	1.7	0.5	2.6

C. Means of Trials per Subject to Reach the Criterion of Learning

No-reward period:							
Included		50.7	49.5	58.2	57.8	52.9	58.2
Excluded	47.2	45.7	44.5	48.2	47.8	38.9	43.2

* On the first trial with reward there was food in the goal box, but no food expectation existed.

The *third measure*, which is given in Table 1*B-b*, consists of the number of animals whose errors increased, remained the same, and decreased from the last trial of the prereward period to the first trial of the reward period. Again, the 3-day shifted group has a record different from the others: Seven out of ten subjects made more errors, whereas in all other groups the number ranged from one to three.

The *fourth measure*, which is recorded in Table 1*B-c*, is concerned with an analysis of blind alleys entered. In all groups, except the 3-day shifted one, the number of blinds is reduced on the first trial of the first reward day. Of special interest is the comparison of the 3-day unshifted and shifted groups. On the last trial of the day prior to reward the same number of blinds is entered by both groups. On the next day there is a drop in the number of blinds entered by the group which continued in the same maze, and a rise in the one which was shifted to another maze. The difference between the two groups is significant at the .001 level (Table 2*B*).

A still more striking record of interference in the 3-day shifted group is the number of *new* blinds entered when the maze was shifted. Here, again, the difference between the shifted and unshifted groups is significant at the .001 level. To anticipate our interpretation, the animals had begun to learn the true path on the third unrewarded day, and when the maze was shifted on the fourth day, they continued what were formerly correct turns, but which now led into blind alleys.

In the other groups the records of blinds entered was consistent with those of the other measures with one possible exception. The number of new blinds entered by the 2-day shifted groups was twice as large as that of the unshifted group. The difference was barely significant at the .05 level. However, the total number of blinds entered decreased as it did in the other four groups.

TABLE 2

Significance of Differences

VARIABLES	1-DAY GROUPS			2-DAY GROUPS			3-DAY GROUPS		
	Diff.	t	p	Diff.	t	p	Diff.	t	p
A. Between means of errors on last day unrewarded, and first day rewarded in:									
Unshifted groups	6.8	7.4	.001	6.4	5.5	.001	5.3	5.0	.001
Shifted groups	7.2	5.0	.001	5.3	3.1	.01	1.4	0.9	
B. Between unshifted and shifted groups:									
Means of errors on first rewarded day	0.3			0.7			−4.2	2.7	.02
Means of blinds entered:									
On first trial of first rewarded day	0.3			0.7	1.4		−1.9	9.6	.001
New on this first trial	0			−0.8	2.1	.05	−2.1	10.0	.001

C. Between means of errors of unshifted 1-day and 2-day groups on second day of training (rewarded vs. unrewarded):

$$D = 11.6 - 16.3 = 4.7 \qquad t = 2.24 \qquad p = .02$$

and between unshifted 2-day and 3-day groups on third day of training (rewarded vs. unrewarded):

$$D = 9.9 - 13.2 = 3.3 \qquad t = 2.24 \qquad p = .05$$

D. Between one day and the next in the 2-day and 3-day groups during the no-reward period the differences in errors were insignificant with no p better than .20.

During the no-reward period there was a drop in error scores from one day to the next in the 2-day and 3-day groups. The differences are not significant, but they show a definite trend (Table *2D*). Relevant to this record is the observation that along with the decline in total errors went a reduction from day to day of the number of immediately repeated entries of blind alleys in the same trial. When all five trials per day were considered, it was found that on the first day the 2-day groups had 102 such repetitions, and on the second day, 88. The 3-day groups had 111, 88, and 57 repetitions, respectively, on their first three no-reward days.

The means of the trials required to reach the criterion of learning are given in Table *1C*. If one compares the control, 1-day, and 2-day groups, the striking fact seems to be that the length of the learning period when measured from the introduction of reward is the same in these three groups. It is lower in the unshifted 3-day group, and this is what one should expect if learning the correct pathway did start before introduction of reward, as indicated by negative transfer in the shifted group. Contrariwise, one should expect the number of trials in the shifted 3-day group to be the largest, which is not the case. All of these results on trials indicate mere trends inasmuch as the differences are not statistically significant.

Records on running times are not reported because this criterion is not as relevant to the problem as are errors. Differences between the two mazes and between the sexes were found to be minimal and are not reported.

Discussion

Statistical reliabilities on which major conclusions are based in this study are of the .02 level of confidence or better. If the small samples of ten in each group and the large individual differences of the subjects are considered, it seems that any level poorer than .02 would hardly be acceptable.

Negative transfer occurred only in the shifted 3-day group. Whatever was learned during the no-reward period interfered with running in the new maze in this group but not in the 1-day and 2-day groups. The conclusion seems justified that this learning involves the correct pathway because it is only the learning of the correct path that can produce negative transfer when the path is altered. Another conclusion would be that this learning takes place largely at a late phase of the no-reward period.

In the 2-day shifted group there is only one slight indication of interference. The number of new blinds entered on the first trial of the third day, when the maze was shifted, was almost twice that of the unshifted group (Table 1*B*). But all other measures indicate absence of negative transfer: The number of errors on the third day was smaller than on the second day; the number of errors on the first trial of the third day was smaller than on the last trial of the second; and the number of subjects whose errors decreased or stayed the same was seven out of ten. It would therefore seem safe to conclude that learning of the true path did not occur during the no-reward period of the 2-day shifted group. However, one should bear in mind that the 6-unit maze used may not be as sensitive an instrument as a larger one might have been (6) and that a more sensitive instrument might have detected learning of the true path at an earlier stage.

Learning during the no-reward period was clearly observable, as it has been in other studies of the Blodgett-type situation summarized by Thistlethwaite (6). That the things learned at this state have to do with general maze experience seems well substantiated (2, 4). Especially relevant here are the observations of MacCorquodale and Meehl "that when special precautions are taken to avoid giving any of the usual kinds of reinforcement, the rat nevertheless shows a significant tendency to 'learn' the maze in the sense that when subsequently run in either direction, he tends to avoid the culs." As to the factors producing such general learning, as we have called it, they suggest "that it is difficult to conceive of them as being based on anything other than the differential effects of unimpeded running versus stopping and turning around" (3, p. 371). In the present experiment not only were similar observations made, but additional evidence was seen in the steadily decreasing number of repeated entries into the same blind alleys at any one trial as reported above.

In this experiment we are obviously dealing with two kinds of learning, a general kind which involves things that make subjects maze-wise, and a specific kind which involves the true path. The onset of the two kinds does not seem to coincide, the general kind starting right at the beginning of training and the learning of the true path at a later stage.

Latent learning, that is, learning which is not directly observable and which occurs without reinforcement, must be considered with respect to the two kinds of learning separately. Increased efficiency, in the general kind of learning of how to run in any maze, was clearly observable and evidently manifest even though no reward was provided by the experimenter. What might be the reinforcement for this kind of learning has been suggested by MacCorquodale and Meehl, as quoted above, and also more recently by J. P. Seward (5, p. 140).

It is the specific kind, the learning of the true path, which the results of this study permit us to call latent. The behavior of the subjects during the no-reward periods was the same in all groups. And yet, on the first day of reward, and when the maze was shifted, there was no negative transfer in the 1-day and 2-day groups, but there was in the 3-day group. This result indicates that learning the true path had definitely occurred on the third no-reward day in the 3-day group. Inasmuch as this learning was not observable previously and occurred without obvious reinforcement, we may call it latent. We said "without obvious reinforcement." The reinforcement theorist will, of course, always be able to suggest some kind of need reduction, which may, however, not be capable of experimental demonstration.

On the basis of the evidence another definite conclusion emerges. *A significant drop of errors, when reward is introduced after a period of no reward, cannot as such be considered as evidence of latent learning of the correct pathway.* Paraphrasing this conclusion we might say that one part of our results clearly confirms those of Blodgett, while just as clearly another part contradicts his interpretation. A significant drop of errors occurred on the first rewarded day of the 1-day and 2-day unshifted groups, but it also occurred in the similar shifted groups, which is an indication that learning the true path had not begun prior to this day. The rapid drop of errors (and time) as such has been taken by Blodgett (1) and others (6) as evidence of latent learning. If their explanation is not tenable, as our study indicates, the question arises, What is the reason for a significant error drop when reward is introduced? A plausible answer seems to be that if in the no-reward period there has been only learning of a general kind of how to run in a maze, the introduction of reward will bring about the specific learning of the true path. The hypothesis that this is the major cause for the drop in errors at this stage will be tested in an additional experiment below.

TABLE 3

A. Means of Errors per Subject per Day of Last Four Trials

DAY	REINFORCEMENT	CONTROL GROUP		EXPERIMENTAL	
		Maze	Errors	Maze	Errors
1	No reward		18.4		17.6
2	Reward	same	11.6	same	9.7
3	Reward	same	8.9	shifted	13.6

B. Errors per Subject on Single Trials

	CONTROL GROUP		EXPERIMENTAL	
a. Means of errors:				
On last trial, 2nd day	same	2.3	same	2.4
On first trial, 3rd day	same	1.9	shifted	4.0
b. On 1st trial third day, no. of subjects whose errors:	same	subjects	shifted	subjects
Increased		2		9
Remained the same		4		1
Decreased		4		0
c. Number of blinds entered:		blinds		blind
On last trial, 2nd day	same	2.1	same	1.8
On first trial, 3rd day	same	1.9	shifted	3.2
New on this trial	same	0.7	shifted	2.1

The continuity issue and latent learning are found to appear intriguingly related in this study. The lack of negative transfer in the 1-day and 2-day groups indicates that there was neither continuity in the learning of the correct pathway, nor was there any latent learning under no-reward conditions during the first ten trials. It was only after the next five trials of the 3-day groups that both continuity and latent learning were brought to light. This result might suggest that whenever latent learning of the true path occurs, continuity is necessarily present, and that whenever such latent learning is absent, continuity is also absent.

TABLE 4

Significance of Differences

VARIABLES	CONTROL GROUP			EXPERIMENTAL		
	Diff.	*t*	*p*	Diff.	*t*	*p*
a. Means of errors:						
Between days 1 and 2..........	6.8	7.4	.001	7.9	7.9	.001
Between days 2 and 3..........	2.7	5.0	.001	−3.9	2.54	.03
Between last trial of 2nd day and first trial of 3rd day..	0.4	.95		−1.6	4.7	.001
b. Between control and experimental on first trial of 3rd day:						
Means of errors....				−2.1	4.5	.001
Means of blinds entered.........				—1.3	2.6	.02
Means of new blinds entered..........				−1.4	2.78	.02

AN ADDITIONAL EXPERIMENT

In the preceding discussion it was noted that there occurred a significant drop of errors on the day the subject found food in the goal box, even if the true path of the maze had not been learned on the preceding one or two days without reward. It was suggested that the introduction of reward in such a case might start the learning of the true path.

In order to test this hypothesis, another experimental group of rats was given training similar to that of the old 1-day unshifted group. Like this group, which may be considered as the control, the new group was given no reward on the first day followed by reward on the second day in the same maze, but unlike the control, it was shifted to the other maze on the third day, after which it was continued with unchanged conditions for two more days.

In terms of errors, the experimental and control groups were alike on the first two days. On the second day, when reward was introduced, both showed a significant error drop. It was on the third day of training, when the maze was shifted in the experimental group, that its error score rose as predicted, while the errors of the control group continued to drop. The rise in errors on four trials from the second to the third day just misses being significant at the .02 level (t is 2.54 instead of the required 2.55), whereas the rise from the last trial of the second day to the first trial of the third day is significant at the .001 level. Of special interest again is the number of new blinds entered on the first trial of the third day which is larger than the total number of blinds entered on the last trial of the second day, that is, 21 as against 18 (Tables 3 and 4).

These results may be interpreted as follows. The negative transfer caused by the shifting of the maze in the experimental group after one day of reward indicates previous learning of the true path. That this specific learning had not started already on the first day of training when no reward was given was demonstrated in the original experiment by the 1-day shifted group which showed no negative transfer. That this specific learning would not have started on the second day of training without reward was demonstrated by the 2-day shifted group which did not show negative transfer. It must therefore have been the introduction of reward on the second day of training that started the learning of the true path.

Considering the records of these groups and the special conditions of the experiment, we may conclude that if there has been no learning of the true path on the unrewarded five trials of the first day, the introduction of reward on the second day of training will bring about the beginning of such learning, but the further withholding of reward will not do so.

We do not claim that the introduction of reward was without effect upon the efficiency of what we have called the general kind of learning. Quite obviously, however, its more striking effect was upon the learning of the true path.

The additional experiment was necessitated by some of the results of the main experiment. Using a theoretical approach, J. P. Seward has recently been led to state that "the reinforcement theorist still has to explain the sharp elimination of errors which sometimes accompanies" the introduction of reward (5, p. 140). We submit that a partial explanation is suggested by the results of this experiment.

SUMMARY

The general purpose of this study was to test the occurrence of latent learning during the no-reward period in a Blodgett-type situation by shifting one half of the subjects, when reward was introduced, to a new maze whose floor plan was a mirror image of the one in which training began. There were three periods of no-reward, one, two, and three days of five trials each. For each period there were two groups of ten naive hooded rats on a 22-hr. food deprivation regime: one of the groups was shifted to a new maze on the day of introduction of reward while the other one was continued in the old maze. A control group was trained with reward from the start.

Negative transfer occurred only in the group that had been trained with no reward for three days. In the 2-day and 1-day no-reward groups the performances of the animals that were shifted to a new maze and of those that were not shifted, were alike in showing the same significant reduction of error when food was introduced.

The following conclusions were reached:

1. Manifest learning which was observed from the start, during the no-reward period of the first days, was of a general kind which is best characterized by saying that the subjects were becoming maze wise.

2. The learning of the correct pathway was latent; it could be detected only through negative transfer and occurred at a later stage in the no-reward period.

3. Taken by itself, the reduction of errors, when reward is introduced, is no proof that latent learning has occurred during the no-reward period.

The question of how to account for the significant error drop on the first day of reward in the one-day and two-day no-reward groups was answered by an additional experiment, the results of which indicate that introduction of reward starts the learning of the true path, when continuance of no-reward would not do so at this phase of training.

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THE EFFECT OF MAGNITUDE OF REWARD ON MAZE LEARNING IN THE WHITE RAT

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Among problems in contemporary learning theory few have been more elusive than the role which is to be assigned to rewards. In Hull's *Principles of Behavior* (2, p. 131) we find that habit strength, $_{S}H_{R}$, is a positive growth function of the magnitude of the reinforcing agent. However, in the 1949 revision of the postulates (3) $_{S}H_{R}$ is no longer determined by the magnitude of the reinforcing agent; the latter now enters directly into the equation for reaction potential, $_{S}E_{R}$. Seward (8) has recently written a critical review of the literature pertaining to the role of rewards in learning and performance.

In a number of previous studies it was found that simple locomotor performance is a function of the magnitude of reward (1, 9, 10). Similarly, Reynolds (7) reports that the learning of a simple T maze proceeds more rapidly with a 160-mg. pellet as an incentive than with a 30-mg. pellet. However, in a black-white discrimination problem (6) no such differences in the rate of acquisition could be observed. Reynolds accounts for these differences in terms of an *R*-hypothesis, which states that only in the case of learned responses which are replicates of the final response to the reinforcing agent is the amount of reinforcement a factor. The running response in a T maze is considered to be a replicate of the final response to the reinforcing stimulus. Seward (8) criticizes the equivocal nature of this hypothesis.

Search of the literature failed to disclose any studies in which the quantity of reward was varied in more complex learning situations. The purpose of the present study is, therefore, to determine the effect of varying the magnitude of the reward on multiple-response learning in the white rat.

METHOD

Apparatus

A two-unit linear-alley T maze with swinging nonretrace doors was employed. A floor plan of the maze, indicating the major dimensions, is shown in Figure 1. The sides of the maze were made of pine boards painted black, and the flooring was orange linoleum. The doors were made of Plexiglas and painted black. The entire maze was covered with hardware cloth.

Half the *S*s in each experimental group to be described below were trained to run through the maze on a left-right pattern, the other half on a right-left pattern.

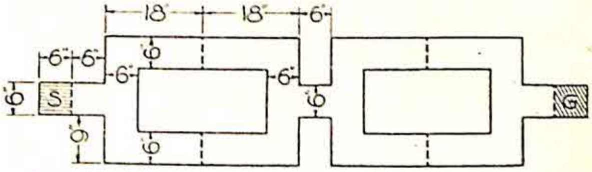

FIG. 1. Floor plan of the maze. Key: *S*, starting box; ---, door; *G*, goal box.

Subjects

One hundred and thirty naive albino rats, including males and females, 60 to 110 days old at the start of the experiment were used in this study. The *S*s were obtained from the colony maintained by the Home Economics Department at the University of Tennessee.

The *S*s were maintained on an approximately 22-hr. food-deprivation schedule. They received a total of 9 gm. of Purina Dog Chow daily. This included the amount fed during training.

Procedure

In an initial experiment two groups of *S*s, one receiving 2,500 mg. and the other 250 mg. of food reward were tested. Since the performance of the two groups was similar, additional groups with differing amounts of reward were tested. This paper reports the pooled data obtained from several experimental series.

Preliminary training. The *S*s were pretrained in an 18-in.-long runway which was constructed exactly like the maze alleys described above. A nonretrace door, like the doors in the maze, was suspended at the entrance to the goal box, which was similar to the one used in the maze. The *S*s were first given several trials with the doors open; next, the doors were pushed open by *E*; and, finally, *S*s were trained to push the doors open themselves. The groups which during the training trials ran to a 2,500-mg. and to a 250-mg. incentive, respectively, received a 250-mg. pellet in the goal box, while the groups which ran to a 75-mg., 20-mg., and 0-mg. incentive, respectively, received a 75-mg. pellet.

Several training trials were given daily for four days. At the end of this training period all *S*s which were to be used in the experiment were proficient in pushing the doors open.

Training. Prior to training *S*s were assigned at random to various reward groups. Initially there were 41 *S*s in a 2,500-mg., 29 in a 250-mg., 42 in a 75-mg., 31 in a 20-mg., and 12 in a 0-mg. incentive group. However, during the course of training several *S*s (proportionately more in the smaller-reward groups) were traumatized when their heads got caught under the swinging doors. These *S*s were removed from the study. A total of 37 *S*s in the 2,500-mg., 26 in the 250-mg., 34 in the 75-mg., 22 in the 20-mg., and 11 in the 0-mg. reward group completed the training series.

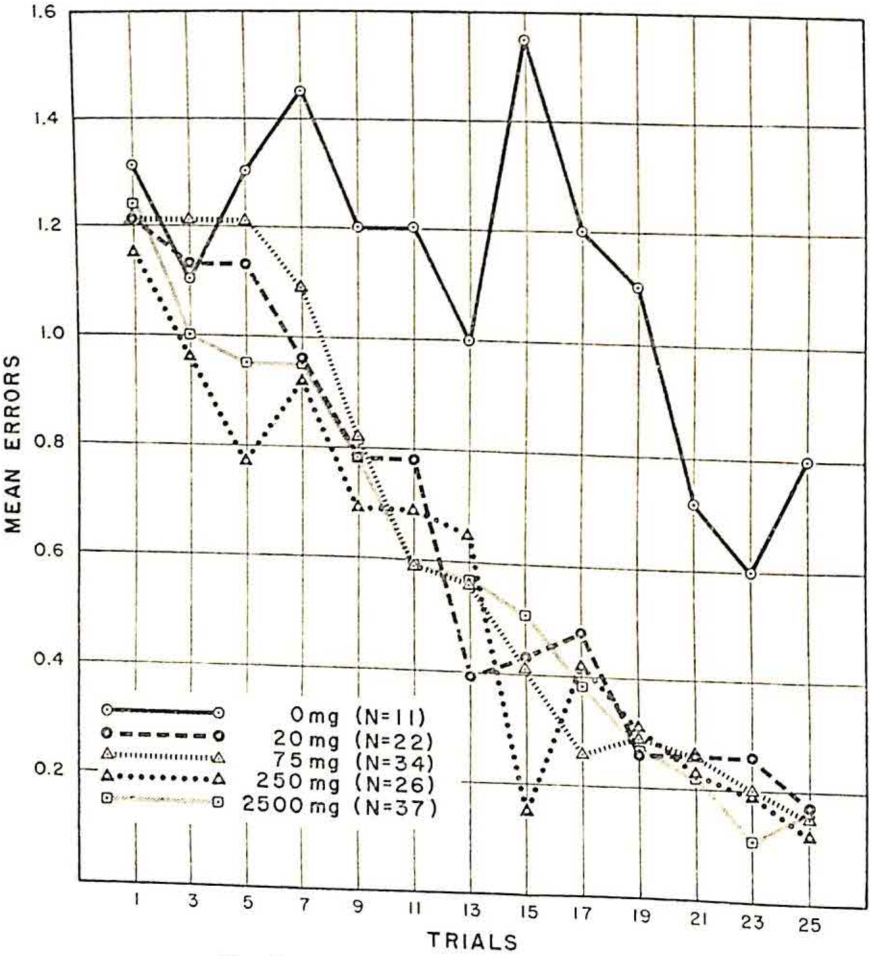

FIG. 2. Mean number of errors per group

Each *S* received one trial per day until it reached the criterion of three consecutive errorless trials, after which it was removed from the training series but was kept on the records as having made zero errors on subsequent trials. All training was discontinued after 25 days.

The incentives used were dry Purina Dog Chow pellets of a size appropriate for each experimental group. After *S* had consumed the reward in the goal box, it was returned to its home cage where it was fed its daily ration about 1 hr. after completing its training trial.

RESULTS

Figure 2 presents the mean number of errors per *S* for the training series. It is quite apparent that the learning speeds of the four experimental groups were very similar. It may also be seen that it was the food pellet which acted as the main incentive for learning, for the 0-mg. group, which otherwise received the same treatment as the rewarded groups, showed a much slower progress in error elimination. That the control group should also exhibit some learning is not surprising in view of previous similar findings by MacCorquodale and Meehl (4).

Aside from the total number of errors, another indicator also argued for the basic similarity in the learning rates of the experimental groups. Seventy-five per cent of the 2,500-mg., 76.9 per cent of the 250-mg., 76.5 per cent of the 75-mg., 77.3 per cent of the 20-mg., and only 18.2 per cent of the 0-mg. group attained the criterion of three consecutive errorless trials during the training period. The average number of trials required for

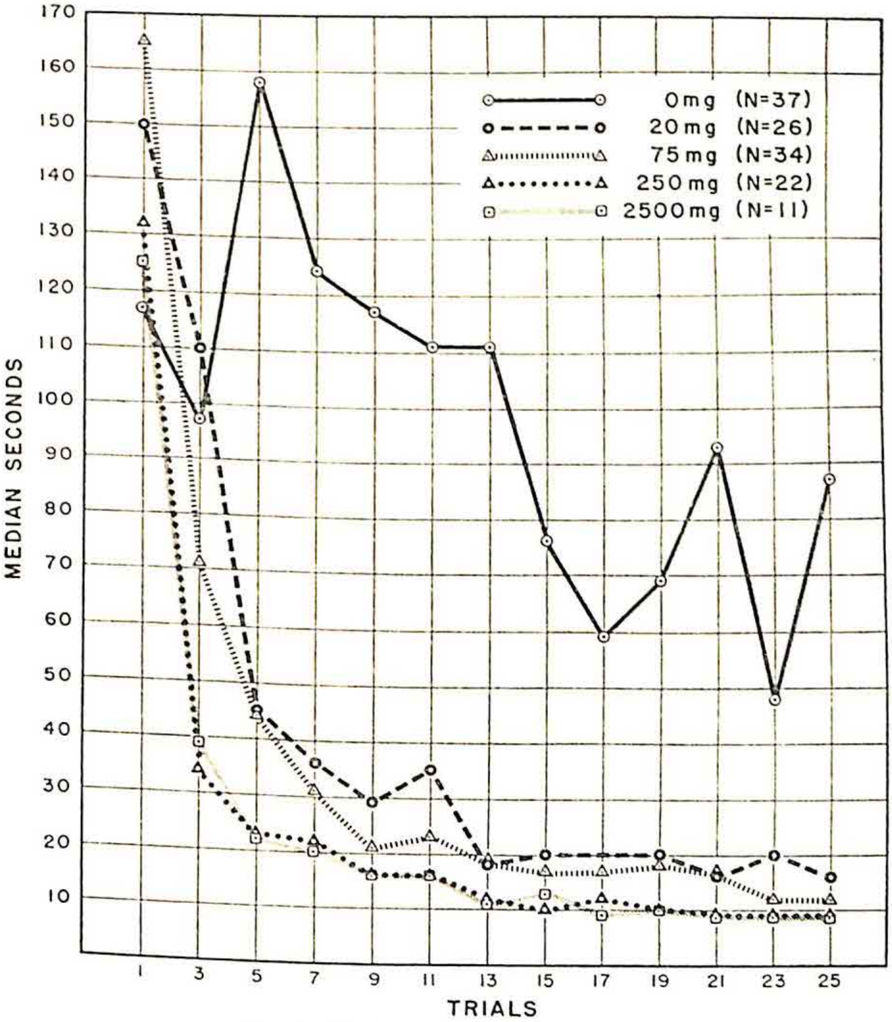

FIG. 3. Median time scores per group

those *S*s that did reach the criterion was 15.7 for the 2,500-mg. group, 14.6 for the 250-mg. group, 15.3 for the 75-mg. group, and 16.1 for the 20-mg. group.

Figure 3 represents the median time scores for the five groups. Since the data do not meet the necessary assumptions for a *t* test of statistical significance, the nonparametric Mann-Whitney *U* test (5) was applied between the various groups, using the time scores for Trials 10, 15, 20, and 25. The results of this analysis are summarized in Table 1.

It may be seen that the differences in time scores between the 2,500-mg. and the 250-mg. groups and the differences between the 75-mg. and the 20-mg. groups are not significant. However, the differences between either of the two large-reward groups and the two smaller-reward groups do show a definite trend in favor of the larger-reward groups.

TABLE 1

Results of Significance Tests for Time Scores

GROUPS COMPARED	TRIAL NO.							
	10		15		20		25	
	ND*	p	ND	p	ND	p	ND	p
20-mg.–75-mg....	0.89	.27	1.04	.23	0.32	.38	0.29	.38
20-mg.–250-mg...	2.28	.03	3.04	.001	2.65	.01	2.93	.01
20-mg.–2500-mg..	2.07	.05	5.10	1×10^{-6}	4.68	1×10^{-5}	3.31	.002
75-mg.–250-mg.	1.43	.14	2.49	.02	2.12	.04	2.94	.01
75-mg.–2500-mg.	1.45	.14	2.00	.06	2.96	.01	3.15	.002
250-mg.–2500-mg.	0.31	.38	0.56	.34	1.54	.12	0.07	.40

* These are normal deviates. The p values are for a one-tailed test.

DISCUSSION

The results would seem to indicate that in learning situations of the complexity level represented by this study, the amount of incentive does not influence rate of learning, measured in terms of errors, as long as the incentive exists above a certain threshold value.

The present findings are not in accord with the data reported by Reynolds (7) for the learning of a single-unit T maze. In our study there were no differences in the learning rates of the experimental groups even though the running times for the small-reward groups were significantly higher than those for the large-reward groups. Thus, the *R* hypothesis, which postulates a positive relationship between amount of reinforcement and the acquisition of a turning response, could not be verified in the present experiment. Apparently, in a multiple-response learning situation other factors contribute more toward the acquisition of a habit than the magnitude of the reward.

The differences in the running times between the two large- and the two small-reward groups would seem to represent differences in performances which do seem to be affected by the magnitude of the incentive. This is consistent with the runway data of Crespi (1) and Zeaman (10). Actually, difference between the magnitudes of the incentive values has to vary considerably, especially when the quantities are considerably above threshold values, before a difference in performance may be observed. In our experiment the running times of the 250-mg. group were no different from those of the 2,500-mg. group.

The results tend to support Hull's revised Postulate IV (3), which states that rate of habit formation, or $_SH_R$, is not a function of the magnitude of the incentive.

However, it should be pointed out that the quantity of primary reinforcement which was sufficient to produce a marked change in the rate of learning between the experimental and the control groups was quite small, constituting only about .002 of *S*s' daily food intake.

SUMMARY

One hundred and thirty albino rats received one daily trial on a two-unit linear T maze under a 22-hr. food-deprivation schedule. Thirty-seven *S*s received a 2,500-mg. food reward, 26 a 250-mg., 34 a 75-mg., 22 a 20-mg., and 11 a 0-mg. reward. Rate of learning, measured in terms of total number of errors, proportion of *S*s that reached a criterion of three consecutive errorless trials, and the average number of trials it took to reach the criterion, were similar for all groups receiving a reward, but varied significantly from the control group which received no food reward. However, the running speeds of the 2,500-mg. and the 250-mg. groups differed significantly from the speeds of the 75-mg. and the 20-mg. groups.

The data indicate, therefore, that in learning situations such as that described in this paper, rate of learning is not determined by the magnitude of the incentive. This is in agreement with Hull's revised Postulate IV.

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INCENTIVE SIZE, FOOD DEPRIVATION, AND FOOD PREFERENCE[1]

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This experiment is the second of a series, and is part of a systematic investigation of monkey food preferences. It examines the relations among variables of food deprivation, quantity of incentive, and quality of incentive. These three presumptive or demonstrable determinants of the effectiveness of a reward are manipulated simultaneously, and concurrent changes in preference are ascertained by observations of behavior in a choice situation.

METHOD

Subjects

Nine adult rhesus monkeys were *S*s for this investigation. Of the group, three were males (no. 147, 150, 153), three were females (no. 137, 146, 151), and three were pregnant females (no. 140, 142, 143). All had had extensive test experience, which included participation in at least one preference experiment.

Apparatus

The experiment was performed with the Wisconsin General Test Apparatus (2, Fig. 1). It consists of a restraining cage, an adjacent table, and a superstructure which supports movable opaque and one-way vision screens. A test tray which runs on rails mounted upon the table can be moved toward or away from the monkey, which is placed inside the cage. The tray used for this investigation measured 9 by 24 in. and was painted light gray. Near the forward edge of the tray were two rectangular food wells spaced 5 in. apart, each 2½ in. long, ½ in. wide, and 1/16 in. deep.

Procedure

The preferences of each monkey for peanut, bread, potato, and celery were first scaled by a method of paired comparisons. The size of a peanut defined a standard to which pieces of other kinds of incentive were cut. The incentives were presented to *S*s in pairs, and records were taken of the choices made. Further details of this procedure are given elsewhere (3). Scale values were computed by the method described by Guilford (1, p. 236). Once the orders of preference for these foods were established, two kinds were selected for subsequent use. These were the most preferred and the second least preferred food for each *S*. Invariably potato was the second least preferred food. Eight *S*s ranked peanut at the head of the list; the ninth *S* preferred bread.

In the first phase of the experiment proper, five different amounts of peanut (or bread, for one monkey) were paired with two different amounts of potato, and the choices of *S* were recorded. On each trial the appropriately sized rewards were placed in the food wells while *S* watched. Then the one-way vision screen of the apparatus was lowered in front of *E*, and the test tray was moved to within *S*'s reach. As soon as *S* chose one of the two foods, the test tray was rapidly withdrawn. If a particularly agile *S* succeeded in removing both foods, the one picked first was recorded as the choice.

The fractional amounts of peanut were prepared by splitting a whole nut in half, then dividing each half lengthwise, and then dividing each fourth into two or four pieces. Quantities of 1, ½, ¼, ⅛, and 1/16 peanut were compared with 2 or 4 pieces of potato cut to the size of a whole peanut. Pieces of bread for the one *S* that ranked this food first were of the same sizes as the five different quantities of peanut. Each of the ten possible combinations of sizes was presented five times in random order on each of the eight days of testing. Preferred and nonpreferred food appeared an equal number of times in right and left positions. All *S*s were tested between 12:00 M. and 4:30 P.M. The time of maintenance feeding was 6:00 P.M.

The testing technique for the second phase was the same as that for the first, but an additional variable was introduced. Time of maintenance-food deprivation was manipulated by procedures similar to those outlined by Meyer (4). Each *S*'s daily ration was 160 gm. of Purina Laboratory Chow, 70 gm. of carrot, and ½ orange. Preference testing was introduced 1, 23, and 47 hr. after feeding. The extraneous variables of deprivation sequence, *E*, and sexual status were controlled by counterbalancing. A total of 50 comparisons were presented to each *S* on each of 12 test days. The 12 test days were spaced 2 days apart regardless of the duration of deprivation preceding the experimental session.

RESULTS

The data collected in the first phase are summarized in Table 1. This shows the per cent choice of the preferred food for each size combination at different stages of practice. Each cell score is based upon ten comparisons, and the data for all nine *S*s have been pooled. The principal conclusion to be drawn from these scores at the moment is that changes in preference with learning are negligible. It should be remembered that these *S*s had had

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[1] This research was supported in part by the Research Committee of the Graduate School from funds supplied by the Wisconsin Alumni Research Foundation.

[2] Now at the University of Indiana.

previous experience with the foods, and hence this stability does not necessarily support the view that such changes never take place. In the prior investigation (3) some trends with practice were noted, although they were not marked.

The effects of variation in time of maintenance-food deprivation upon preference can be assessed from the scores which are given in Table 2. Shown is the frequency of choice of the preferred food by each *S* at each degree of deprivation. The combination of all size comparisons followed an initial analysis which showed similar effects throughout. There is no support for the conclusion that deprivation alters preference. There is a tendency among the means for a greater preference of the preferred food at 23 hr., but this change is slight and insignificant statistically.

TABLE 1

Per Cent Choice of Preferred Food As a Function of Sizes Compared and Days of Practice (Combined Data, Nine Monkeys)

UNITS OF NONPREFERRED AND PREFERRED FOODS COMPARED	DAYS				
	1–2	3–4	5–6	7–8	Total
2–1	92.2	95.6	93.3	96.7	94.4
2–½	73.3	76.7	83.3	70.0	75.8
2–¼	33.3	34.4	26.7	18.9	28.3
2–⅛	5.6	1.1	4.4	5.6	4.2
2–1/16	2.2	0.0	0.0	1.1	0.8
4–1	71.1	77.8	82.2	71.1	75.6
4–½	25.6	24.4	25.6	20.0	24.0
4–¼	10.0	16.7	7.8	3.3	9.4
4–⅛	0.0	0.0	1.1	1.1	0.6
4–1/16	1.1	0.0	0.0	0.0	0.3

TABLE 2

Frequency of Choice of Preferred Food As a Function of Time of Maintenance-Food Deprivation

HOURS OF DEPRIVATION	MONKEY NUMBER								
	137	140	142	143	146	147	150	151	153
1	13	54	44	41	119	62	57	37	88
23	79	53	63	38	179	61	106	52	48
47	30	48	47	37	86	62	66	57	47

Since neither learning nor deprivation were found to affect performance scores, the first- and second-phase data were combined for analysis of the effects of size ratio upon selection. The outcome is illustrated in Figure 1. This graph depicts per cent choice of peanut or bread as a function of the ratio between the sizes of the preferred and nonpreferred foods. Open circles summarize comparisons between preferred foods and 4 pieces of potato, while closed circles show the results obtained when 2 pieces of potato were employed. Thus a ratio of 1/64 means that 4 pieces of potato were offered together with 1/16 peanut or its equivalent. At the other end of the scale, the ratio of ½ is obtained when 2 pieces of potato appear with 1 peanut or its equivalent. Two scores are available for intermediate ratios. For example, the ratio ⅛ is either ¼ peanut versus 2 pieces of potato or ½ peanut versus 4 pieces of potato. It is evident from the graph that equivalent-size ratios yield equivalent performance, and thus that absolute magnitudes or absolute differences in magnitude are of relatively little significance.

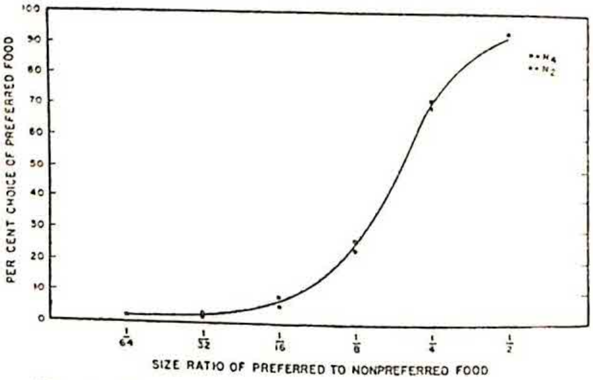

FIG. 1. Per cent choices of the preferred incentive as a function of the ratio between the sizes of the compared foods. The open circles summarize comparisons between preferred food and four pieces of potato; the closed circles represent the scores obtained when two pieces of potato were used.

DISCUSSION

In the first experiment of this series, Harlow and Meyer (3) found that different amounts of peanut are judged equidistant in preference by monkeys if the quantities form a logarithmic series. Thus any pair of incentives with a given size ratio is separated by the same number of scale units, and the preference of the larger over the smaller amount is always the same regardless of the absolute magnitudes. The present study confirms and extends this conclusion.

If we assume that a quantitative law worked out for peanut is applicable to potato, doubling the amount of this incentive should yield a change of one scaled quantitative preference unit. If the qualitative differential is maintained unchanged with variations in magnitude, the resulting increase in potato preference should be offset exactly by an analogous increase in the amount of peanut. The data show unequivocally that this is so, that the preference behavior evoked by two dissimilar incentives is constant so long as the ratio of their sizes is constant. From this it would seem to follow that quality and quantity are independent determinants of choice frequency. The conclusion is not affected by alteration of time of maintenance-food deprivation.

SUMMARY

This experiment examined the relations among variables which determine the effectiveness of monkey food rewards. The preferences of nine rhesus monkeys for peanut, bread, potato, and celery were first scaled by a method of paired comparisons. Subsequently, two of these foods, the most preferred and second least preferred for each *S*, were presented in varying quantities to the *S*s for choice. Preference was measured as a function of five levels of preferred food and two levels of nonpreferred food. In one part of the study, time of maintenance-food deprivation was varied from 1 to 47 hr.

It was found that preference is related to the ratio of sizes of two incentives even if they differ in quality as well as in quantity, and this relation is unaffected by time of deprivation. These results confirm the conclusion that logarithmic increments in quantity of incentive yield linear increments in scaled preference, and indicate that quality and quantity are independent dimensions.

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THE RELATIVE IMPORTANCE OF COLOR AND FORM IN DISCRIMINATION LEARNING IN MONKEYS

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In 1925 Revesz (7), using *Macaca mulatta* monkeys, reported that his animals showed a slightly stronger preference for form than for color in discrimination learning. This finding was criticized by Harlow (1), who demonstrated that color cues were significantly more effective than form cues as aids in the solution of discrimination problems in his macaques.

The following investigation was therefore undertaken, using methods more closely resembling those of Revesz than those of Harlow. In addition, an attempt was made to discover, when both color and form variables were present in the same discrimination task, whether there was any simultaneous learning of both cues, even when one was dominant.

METHOD AND RESULTS

Subjects

Four monkeys were used in this experiment: two *Macaca nemestrina*, Port and Gin; and two *Macaca mulatta*, Whisky and Brandy. All were preadult, and, while the two *nemestrina* had had some previous experience with discrimination tests, this was not so in the case of the others.

Apparatus and Training

For training, the *S* was placed in a cage, one side of which consisted of a metal sheet. Attached to this was a metal training box with a vertical shutter which could be raised to enable *S* to see and manipulate the apparatus.

The apparatus itself consisted of a rectangular Klüver form board 2 by 9.5 by 28 cm., painted black, in which were two wells 2 cm. in diameter and 12.5 cm. apart. Four stimulus objects were used, a red and a blue equilateral triangle with 6.5-cm. sides, and a red and a blue 5-cm. square, made of three-ply wood and painted with flat paint.

In total area the triangle is slightly smaller than the square. This difference in area is deliberate, because it was found that an equilateral triangle equal in area to a 5-cm. square gave the illusion of greater size and, if employed, might have resulted in *S*'s discriminating by size, which monkeys can do easily.

The two *S*s without previous experience on the apparatus were first accustomed to it by being allowed to take food out of the uncovered wells.

When this was done readily and they were no longer alarmed by the raising and lowering of the shutter, one well was baited and both were covered by identical white circles. As the position of the bait was varied, the *S* was in this way trained to move aside one or, if necessary, both objects until it obtained the bait.

As soon as this was done without hesitation, the training to the stimulus objects used in the experiment was begun. These were divided into two pairs: (*a*) a red triangle with a blue square, and (*b*) a blue triangle with a red square. Thus, whichever pair was used, the two stimulus objects differed from each other in both color and form, so that in learning to discriminate between them the cues of color and of form were presented to *S*. All four combinations of the pairs of these stimuli, offering the two differential cues, were employed as shown in Table 1.

During training the positive stimulus only was baited, and care was taken to exclude auditory and olfactory cues throughout the experiment. The position of the positive stimulus was varied in the order—*RLRRLRRLLL* (*R* = right, *L* = left) and then reversed *RRRLLRLLRL*.

The correction method was used throughout the training of all the *S*s; when they had made the correct choice, they were allowed to investigate the negative stimulus if they wished to do so before the shutter was lowered. This investigation of the negative stimulus occurred very frequently in the early stages of training, but tended to be abandoned when the discrimination was learned.

Training was given each day for five successive days until ten consecutive correct choices had been made. Two *S*s made no error after the second day, and two, none after the third day.

Test 1

Procedure. On the fifth day of training, immediately after making ten correct choices with the training pair of stimuli, *S* was presented with the other pair. This meant that it was confronted with one stimulus which had the positive color and the negative form and one which had the negative color and the positive form of the pair to which it had been trained.

For instance, Port, trained to choose the red triangle and reject the blue square, was confronted in the test by the blue triangle (positive form and negative color) and the red square (positive color and negative form). The same was done *mutatis mutandis* in the case of the other three *S*s.

In all four tests the position of the stimuli was changed in accordance with the formula used during training, and in every case both were baited for the first five trials and thereafter only the one the *S* had chosen five times; altogether, ten trials were given. Having obtained the bait from the first stimulus object, the *S* was not allowed during the test to investigate the other.

Results. The result of this test is that on trial 7 Brandy chose the stimulus whose form was the same as the training object but whose color differed. On the other trials for Brandy, and on all trials for the other three animals, all choices were to the stimulus object of the same color as, but different in form from, the one to which the *S* was trained.

Test 2

Procedure. From the results of test 1 it was inferred that in learning to discriminate between the two stimulus objects used in training, the color cue had been the dominant factor for the monkeys. The question now arose as to whether *pari passu* with the learning of the color discrimination there had been any learning of form, which in test 1 had been masked by the dominance of the color cue. It was in order to test the hypothesis that there was also some learning of form that test 2 was devised.

TABLE 1

SUBJECT	POSITIVE	NEGATIVE
Whisky	Red square	Blue triangle
Brandy	Blue square	Red triangle
Port	Red triangle	Blue square
Gin	Blue triangle	Red square

TABLE 2

Whisky	*FFFFFFFOFO*
Brandy	*OFFFFFFFOF*
Port	*FFFFOFFOOF*
Gin	*OFFFFOFFFF*

F = choice of stimulus object of same form as the positive stimulus used in the original training.

O = choice of stimulus object the same form as the negative stimulus used in the original training.

This test, which was always given immediately after test 1, consisted of presenting *S* with a square and a triangle both of the same color as the stimulus object to which it had been trained. For instance, Port, trained to a red triangle positive and a blue square negative, was given for test 1 a blue triangle and a red square, but for test 2 a red triangle and a red square. The testing of the other three *S*s was by the same method.

Ten choices were given in test 2 with both stimuli baited, as was done by Nissen and Jenkins (5), but once *S* had made its choice no investigation of the second stimulus was allowed. The position of the stimuli was varied as before.

Results. The results are shown in Table 2. It will be recalled that test 2 was given immediately after test 1, in which *S* had made a series of choices of an object similar in color but different in form from the stimulus object to which it had been trained. This means that the *F* choices in test 2 represent a change back from the form chosen in test 1 to the form which was positive in the original training, and affords some indication of the strength of the original, but masked, learning of the form discrimination.

DISCUSSION

In monkeys, Revesz reported that he found some preference for form over color in discrimination learning, but more recent experiments by Harlow have suggested that the reverse is the case.

However, the methods used by these two investigators differed somewhat, for Harlow reports that "the performances on the discriminations differing in both color and form and the discriminations differing in color alone were significantly better than those differing in form alone. The results of this experiment indicate that color is a more effective cue than form for macaque monkeys" (1, p. 234). In other words he found that his *S*s learned to discriminate by color cues more quickly than they did by form cues.

On the other hand, Revesz trained his monkeys to take food from a box marked with a yellow circle, using at the same time other boxes marked with a red triangle, a blue rectangle, and a green trapezium as secondary figures. Later, the animal was offered a red circle, a yellow triangle, a blue rectangle, and a green trapezium, and chose the red circle, i.e., in favor of the same form.

Our experiments, though confirming Harlow's findings, are not measurements of the comparative ease with which monkeys learn color and form discriminations, but resemble more closely Revesz' methods and at the same time have certain similarities to the matching experiments with children reported by Katz (2).

Furthermore, the present investigation has been extended to examine whether at the same time that the monkey was learning the color cue it was also learning to discriminate form. The results set out in Table 2 indicate that this is, in fact, the case.

An experiment in many ways similar to ours was conducted by Nissen and Jenkins, who, working with chimpanzees, found that color differences (these authors used black and white) were more effective than size in single-cue tests subsequent to training in which the two variables were combined in a positive stimulus. This finding is in agreement with our results.

Our experiment produced no evidence that our monkeys in their training had a preference for red over blue or vice versa; these colors were deliberately chosen as one from the long wave portion of the visual spectrum, the other from the short, in view of Yerkes' (9) suggestion that in apes there is some preference for color belonging to the shorter wave lengths.

When we consider the problem of color-form preference in the studies of other workers, we find that with birds, Kroh and Scholl (4), and with chimpanzees Kohts (3) and Nissen and McCulloch (6) all report in their subjects the same preference for color over form that Harlow and ourselves have found in monkeys.

Work with children, usually by means of matching experiments, is discussed at length by Vernon (8) who writes: "Numerous experiments have been performed to test the child's interest in color. . . . He is presented with a form which can be matched either with one of the same color or with one of the same form drawn from a group of others. The tendency to match according to color seems to increase up to a maximum at about five or six years of age and then to decrease again. Below four or five years the child may give merely a random judgment; it is incapable of making the discrimination at all according to the results of Segers" (8, p. 183).

It therefore appears that the preference for color over form is found in birds, in animals with color vision, and in young children, but that in older children form usually becomes dominant over color.

Our experiment demonstrates a definite preference for color in monkeys and at the same time shows, by means of test 2, that even for subhuman primates form has significance and is learned simultaneously with color in a discrimination task when both variables are present, though such learning of form is masked by the dominance of the color cue and only revealed by specially designed tests.

SUMMARY

1. Four monkeys were trained to a positive stimulus differing from a negative one in the variables of color and form.

2. They were then presented with two stimuli, one of which combined the previous positive color with the negative form, and the other the negative color with the positive form, and given ten free choices. In three cases the choice in favor of the positive color combined with the negative form was 100 per cent, and in one, 90 per cent.

3. The same *S*s were then given ten choices of two stimuli, one of which had positive color and form from the training series and the other positive color but negative form, the latter being the stimulus they had just chosen in test 1. In three cases the choice in favor of the form positive in training was 80 per cent and in one 70 per cent.

4. It is inferred from these experimental data: (*a*) that monkeys have a preference for color over form in learning a discrimination; (*b*) that during training, although the color cue is dominant, form is learned simultaneously.

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SOLUTIONS OF PATTERNED STRING PROBLEMS BY YOUNG GORILLAS[1]

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Relatively few tests have been devised for *directly* comparing the perceptual capacities of animals at various levels of the phylogenetic scale (5), or even of the same animal at different stages of its development. Still fewer comparative tests have been reasonably well standardized. Solutions of simple patterned string problems have been shown to vary with age during the first year in the human infant (6). Adult chimpanzees solve more complex problems than monkeys do (2, 3, 4, 8), and there is evidence of differences in ability between species of monkeys (4, 8). The purposes of the present investigation were to extend the comparisons to another of the anthropoid apes, the gorilla, and to evaluate further the patterned string problem as a method for measuring psychological development.

Comparative studies of primate behavior have heretofore almost entirely neglected the gorilla (7, 10). The increasing availability of this animal in America has induced Yerkes (10) to plead for an intensification of psychobiological research on this subject, lest the opportunity be lost, perhaps even by extinction of the species.

METHOD

String problems used in previous studies varied from one investigation to another until Finch (2) duplicated the patterns of Harlow and Settlage (4), in order to compare the capacities of chimpanzees and monkeys. In the present experiment we have retained the essential features of the apparatus described by Finch for his second experiment. The string patterns were always arranged and the appropriate string "baited" while the platform was beyond the reach of the *S* and hidden from view by a vertically sliding panel. White sash cord weighted internally with lead pellets was used, the weights serving to hold the strings in position and to facilitate grasping. The diameter of the cord was 2.8 mm. between the pellets and 4 mm. at the position of each pellet. The pellets were spaced at intervals of 8 mm. along the cord.

Finch added one pattern (his pattern 11) to the 10 problems in Series II of Harlow and Settlage. The 11 patterns are diagrammed in Figure 1. An additional final testing condition was added by us in which patterns 4 and 11 were interchanged on successive trials in an irregular balanced order. This testing condition was used with two of our three *S*s.

Subjects

The *S*s for this experiment were three of the four young lowland gorillas, *Gorilla gorilla*, obtained in Africa by zoo Director R. Marlin Perkins for the Lincoln Park Zoo, Chicago, in October, 1948. At that time their estimated ages, as determined by body weight and size, were: Lotus, 2½ yr.; Irvin Young, 2 yr.; Sinbad, 8 mo. The fourth animal in the group, Rajah, estimated age, 1½ yr., was caged together with Lotus. Rajah was not used in the present experiment because Lotus completely dominated the position at the apparatus whenever a problem was presented. Irvin Young and Sinbad were each housed in separate cages.

Procedure

Virtually no preliminary adaptation to the problem was necessary with Irvin Young, who pulled in single, baited strings immediately and promptly chose the correct string when first confronted with problem 1. The other two *S*s were more awkward or more timid. Sinbad was able to grasp the string at the end of one preliminary session, after repeated efforts to scrape or drag it along the board. Lotus required three sessions before fear of the apparatus was overcome.

Sinbad, the youngest *S* on his Series I (Table 1), worked sporadically because of fluctuations in food motivation. Work was twice interrupted, in February and March, 1949, because of colds in the gorilla colony. Following the March interruption more than a year elapsed before the series of problems was begun over again (Series II) with this *S*. Within the second series there were interruptions occasioned by Bushman's failing health, when quiet in the gorilla house was requested.

The dates of all experimental sessions are given in the table. Where motivation sufficed, 50 trials were presented at a single experimental session. A morning and an afternoon session were sometimes given on the same day. Correction was permitted on error trials when disturbance of motivation appeared imminent, or when *S* was too quick to permit intervention. The majority of errors went uncorrected. A problem having an asymmetrical pattern was alternated every 5 trials with its mirror image, as in previous studies. The string to be baited was altered from one trial to the next in an irregular balanced order.

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RESULTS

Table 1 presents the error scores for each set of 50 trials for each subject. Lotus, the oldest of the *S*s, was consistently the most accurate. She always used her left hand for pulling the string. Irvin Young used the right hand exclusively in 7 of the 50-trial sessions, and even in the other 14 sessions used the left hand on only 20 per cent of all trials. Sinbad (Fig. 2) used either hand about equally often, but sometimes showed long "runs" in which one hand was used consistently.

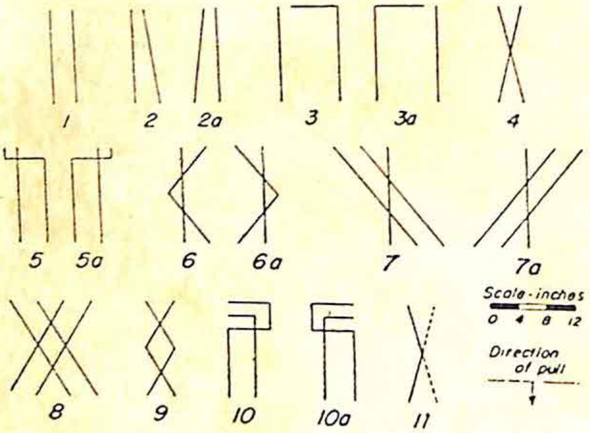

FIG. 1. [Adapted from Finch (2).] The series of 11 patterns used in the present experiment, after Harlow and Settlage, with problem 11 added by Finch. Distances between baited ends of the strings were 2 in. in problems 2, 3, 5, and 10. In all other problems these distances were 4 in. A distance of 15 in. separated the bait hooks from the row of screw eyes which held the ends of the cords nearest the subject.

Problems 10 and 11 proved troublesome for all three *S*s. Only Lotus showed reliably better than chance performance on these two problems for either the first or second session of 50 trials. Problem 11 was at first responded to as a single intersection of strings, i.e., like problem 4, by all three *S*s. This difficulty was overcome by Lotus and by Irvin Young, the latter giving evidence of correct response (19 correct) in the last 25 trials of the 100. This improvement continued in another 90 trials with Irvin before the interchanging of problems 4 and 11 was tried.

Sinbad was poorest in accuracy, in part, perhaps, because he was the least methodical or most playful subject. During both the early and later series playful activity about the cage sometimes intervened for long periods between trials. The final tests (4 and 11 interchanged) were omitted because this *S* was becoming more prone to jerking the strings loose from the apparatus, or playfully refusing to return to the task. (At no time was food

TABLE 1

Error Scores for Groups of 50 Trials

PROBLEM NUMBER	LOTUS (female)*			IRVIN YOUNG (male)†		
	Dates	Trials		Dates	Trials	
		1–50	51–100		1–50	51–100
1	12/27/48	0		12/21/48	(2 in 25)	
2	12/27	0		12/21	(0 in 20)	
3	12/28	0		12/22	8	
4	12/29, 12/30	0	0	12/22, 12/23	18	4
5	12/30, 1/2/49	2	2	12/24	15	12
6	1/6	0	2	12/26	11	11
7	1/8, 1/9	0	2	12/28	6	2
8	1/14, 1/15	0	0	12/29	0	0
9	1/16, 1/22	3	2	12/30	2	9
10	1/24	17	3	1/2/49	22	26
11	1/29	32‡	7	1/6	42§	20
				1/7	17	(3 in 40)
4 and 11 interchanged	2/4	2	3	1/8, 1/9, 1/14	6	10

PROBLEM NUMBER	SINBAD (male)					
	SERIES I**			SERIES II††		
	Dates	Trials		Dates	Trials	
		1–50	51–100		1–50	51–100
1	12/22/48	(7 in 30)				
1	2/5/49, 2/13	15	7	7/17/50, 7/19	8	3
2	2/19, 2/20	1	0	7/21, 7/24	7	7
3	2/26, 2/27	11	11	7/28, 8/18	2	7
4	3/12, 3/13	19	(4 in 15)	8/21, 8/23	10	4
5				8/25, 8/27	12	7
6				8/30, 9/1	13	9
7				10/24, 10/25	16	6
8				10/26, 10/31	6	4
9				11/1, 11/3	5	5
10				11/7, 11/8	21	21
11				11/14, 11/15	36‡‡	29

* Estimated age at start, 33 months.
† Estimated age at start, 24 months.
‡ Errors on all of first 9 trials.
§ Only 3 correct in first 40 trials.
** Estimated age at start, 10 months.
†† Estimated age at start, 29 months.
‡‡ 18 errors in first 20 trials.

deprivation resorted to to increase motivation, as this was against zoo policy.)

The manner of responding by all three *S*s gives only tentative suggestions as to the mode of problem solution. In general, response was a direct reaching for one string or the other promptly after the board was pushed forward, provided *S* was directly in front of the board at the time. Sighting along strings was observed only in a few isolated instances. Occasionally an initial reaching movement was checked, and then redirected or continued, but on approximately 90 per cent of all trials, even with difficult problems, reaching was prompt and direct. On the first problem all *S*s seemed to perceive the food and string continuum as a unit. Even Sinbad, who was first confronted with the apparatus on 12/21/48 and who was then presented with food attached to a single string, "appeared immediately to perceive the relation between the food and the string and turned his attention and efforts to pulling in the string" (to quote our protocols).

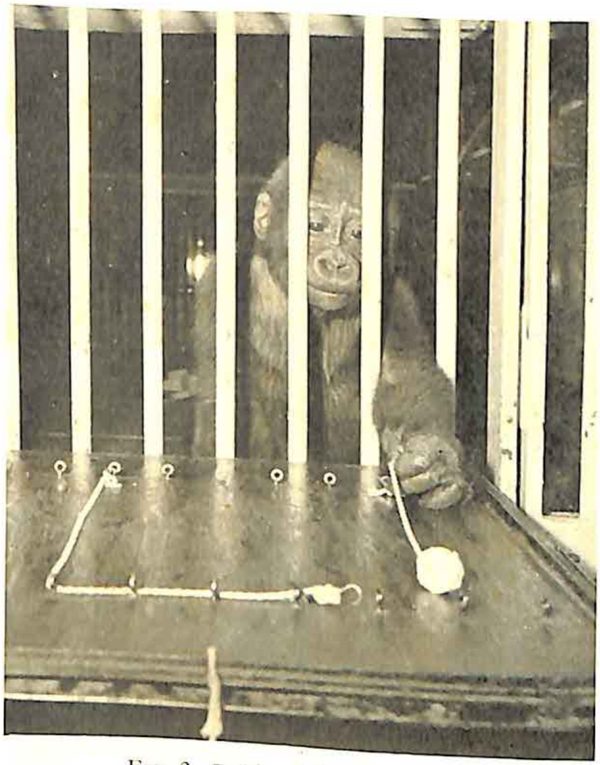

FIG. 2. Subject Sinbad at work

Consistent misperceptions occurred for varying numbers of trials on several of the problems. The difficulty with problem 11 has already been mentioned. On problem 5 all but 2 of the 27 errors made by Irvin Young were pulling the straight string when food was on the crossed string. This error was completely dominant in one of Birch's *S*s (1). On problem 6 Sinbad made 12 of the 13 errors in the first group of 50 trials by pulling the straight string when the food was on the string that crossed and recrossed. Irvin Young showed a tendency in the same direction. On problem 10 all errors made by Lotus were on trials that had the bait on the longer string.

DISCUSSION

Problems 10 and 11 have not been solved by monkeys (4), and these are the most difficult of the series for gorilla and chimpanzee. Problem 9 is much more readily solved by the apes than by monkeys, only one spider monkey having succeeded in the Harlow and Settlage group of 31 monkeys. Problems 5 through 8 do not show a clear hierarchy of differences in difficulty. Our gorillas improved with continued trials on some of the more difficult problems, as did Finch's chimpanzees. Monkeys are reported not to show this improvement with practice (4).

The first four problems were no challenge to Lotus, nor to the better chimpanzee *S*s (2). Comparisons on problems 5 through 11 show that on the total of 700 trials the two best chimpanzees did 93 per cent (Mimi) and 88 per cent (Pati) correctly, while Lotus did 90 per cent. The other two gorilla *S*s did 75 per cent and 73 per cent of these 700 trials correctly, as compared with 86 per cent and 64 per cent for the remaining two chimpanzees. On problem 9 both Lotus and Irvin Young did as well as the best adult chimpanzee's performance. Problem 10 had somewhat less initial difficulty for Mimi and Pati than for Lotus, and two of four adult chimpanzees had less initial difficulty on problem 11 than did Lotus.

Assuming that age is a factor in the performance of the problems used (1, 6), these comparisons must be tentative. The data above suggest that our three young gorillas did almost as well as the adult chimpanzees tested by Finch. The performance by Lotus compares favorably with the best chimpanzee scores. The younger chimpanzees (four to five years of age) in Birch's study (1) did not do as well; however, the numbers of trials per

988

problem were fewer, and the sequence of problems was different. More work is needed before definitive statements can be made concerning the relative abilities of gorilla and chimpanzee, but our data suggest approximately equal ability for these two species on patterned string problems, or possibly a superiority of the gorilla.

It seems quite improbable that differences in visual acuity account, even in part, for differences in performance between individuals and species in this series of problems. Diameters of the strings used are so far above the acuity thresholds of either ape or monkey that the patterned string problems could hardly have constituted an acuity test. Yerkes (9, p. 157) has referred to them as a "test of perception of spatial relation and of adaptive capacity." The exact nature of the perceptual task that is involved, and the factors which show correlations with different levels of performance remain to be worked out.

SUMMARY AND CONCLUSIONS

In a standard series of patterned string problems previously used with monkeys and chimpanzees, three young gorillas showed a range of performances comparable to that of chimpanzees and exceeding that of any species of monkey studied. There is evidence that age as well as phylogenetic level are correlated with performance on these problems. The problems appear to constitute a series of complex visual perceptual tasks rather than tests of sensory acuity.

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DECREMENT OF A LEARNED DRINKING RESPONSE ACCOMPANYING CHANGES IN SEVERAL STIMULUS CHARACTERISTICS[1]

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This investigation was stimulated by the emphasis placed by Guthrie (3) and, more recently, by Estes (1) upon the importance of stimulus-response contiguity in learning. It is related also to the formulation by Estes and Burke[2] of the *stimulus-population* construct.

For Guthrie, learning of a particular movement response in a certain stimulus context takes place upon the occasion of the first occurrence of the movement in that context. He explains "improvement with practice" as a phenomenon observable with complex acts, not with simple movements. Simple movements are learned in one trial; but acts, consisting of combinations of movements which initially are not performed together but must be put together, show improvement over time.

Estes and Burke accept one-trial conditioning between the response occurrence and the immediate stimulus situation. However, *stimulus* and *response* are now explicitly generic notions, event-classes. The immediate stimulus situation is not identical from one occasion to the next; it is a sample drawn from a finite population of stimulus elements. Similarly for the response class. These populations, while ultimately exhaustible over a number of occasions, are not completely available upon any single occasion. And, until both populations are entirely involved in the conditioning relation, maximum response probability is not achieved.

Two further assumptions made by Estes and Burke are: (*a*) Once the environmental situation is fixed, each stimulus element available to the organism is weighted; i.e., it has some fixed probability, θ, of occurring on any trial. (*b*) The behavior of an organism on any trial is a function, not of the entire population of stimulus elements, but only of those stimulus elements which occur on that trial.

If S–R contiguity is as important to learning as these various authors suggest, then we should expect that systematic manipulation of different proportions of a total stimulus situation will result in systematic, quantitative differences in contiguous response measures.

Ferster (2) investigated a problem of this kind in a Skinner-box context using two specified stimulus components. After conditioning bar-pressing behavior in white rats in the presence of an intermittent light and a continuous tone, he attempted to ascertain whether significant differences in extinction measures might be obtained between extinction in the presence of light and tone, and extinction in their absence. He reported no significant differences.

Inasmuch as the present study was conducted before a report of Ferster's work was available, it took a different form. Let us consider an experimental situation in which all the stimulus events are categorized into four classes or components: X, Y, Z, and Q; where X, Y, and Z are specified, and Q is some non-determinable remainder. If some selected response-class, R, is learned in this situation, will the strength of R fall off as X, Y, and Z are systematically varied? Stimulus components X, Y, and Z were defined experimentally as *light intensity, sound intensity*, and *tactual roughness*, and R was *tube drinking* of water.

METHOD

Subjects

The *S*s were 88 male albino rats between 90 and 100 days old at the start of the experiment.

Apparatus

A diagram of one of the experimental boxes is seen in Figure 1. The sides and bottom of the box were constructed of ¼-in. plywood covered on the outside with ½-in. fiberboard. The inside dimensions of the box were 6 in. by 10 in. by 12 in. The Mohr burette-dispenser was held in place by a wooden burette support.

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[1] The authors are indebted to Dr. C. J. Burke, Dr. D. G. Ellson, and Dr. W. K. Estes for advice on various aspects of this study.

[2] Unpublished manuscript. In press, *Psychol. Rev.*

On day 6, Set A and Set B were each broken down into five groups, as indicated in Table 1. In Set A, Group I had no stimulus components changed, Groups II and III each had one component (tactual and sound, respectively) increased, Group IV had both these components increased, and Group V had all three components increased. In Set B, Group VI had no stimulus components changed, Groups VII and VIII each had one component (light and sound, respectively) reduced, Group IX had both these components reduced, and Group X had all three components reduced.

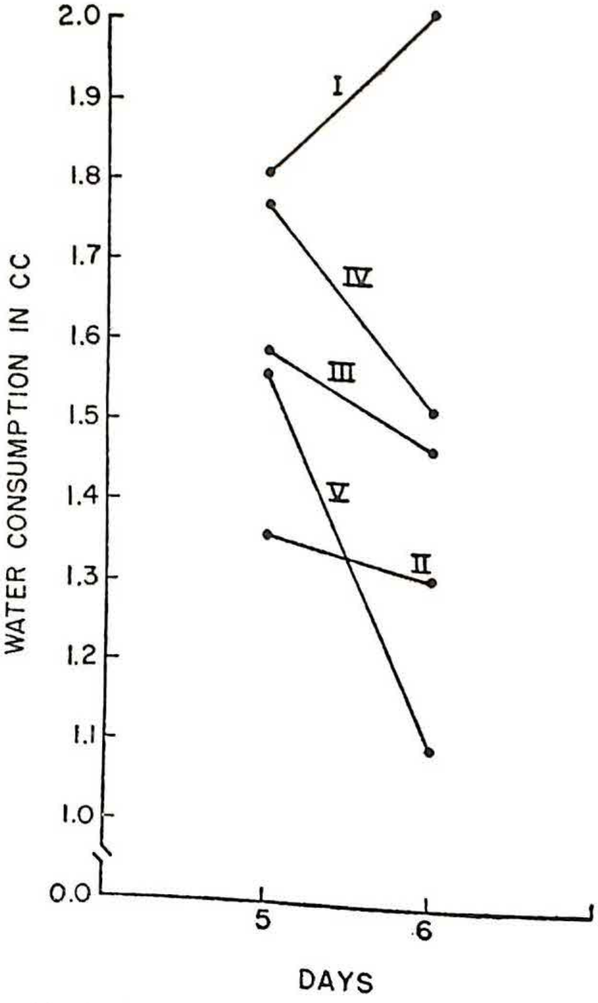

FIG. 3. Comparison of mean amounts of water consumed by groups I to V (Set A) in first 2 min. of experimental session on days 5 and 6.

The tube-drinking response measure was the amount of water consumed in the first 2 min. of the experimental hour.

RESULTS

Figure 2, showing response curves for experimental days 1 to 5, indicates that learning did occur.

Figures 3 and 4 indicate graphically the differences between days 5 and 6. In Figure 3, representing results from Set A *S*s, Group I (control) shows a slight increment in cubic centimeters consumed from 1.8 to 2.0; all the other groups show decrements. It is of interest to note that the lines joining the points for days 5 and 6 have steadily decreasing slopes as we proceed from the group that had no stimulus components changed to the group that had three components changed. Figure 4 shows analogous results for Set B *S*s.

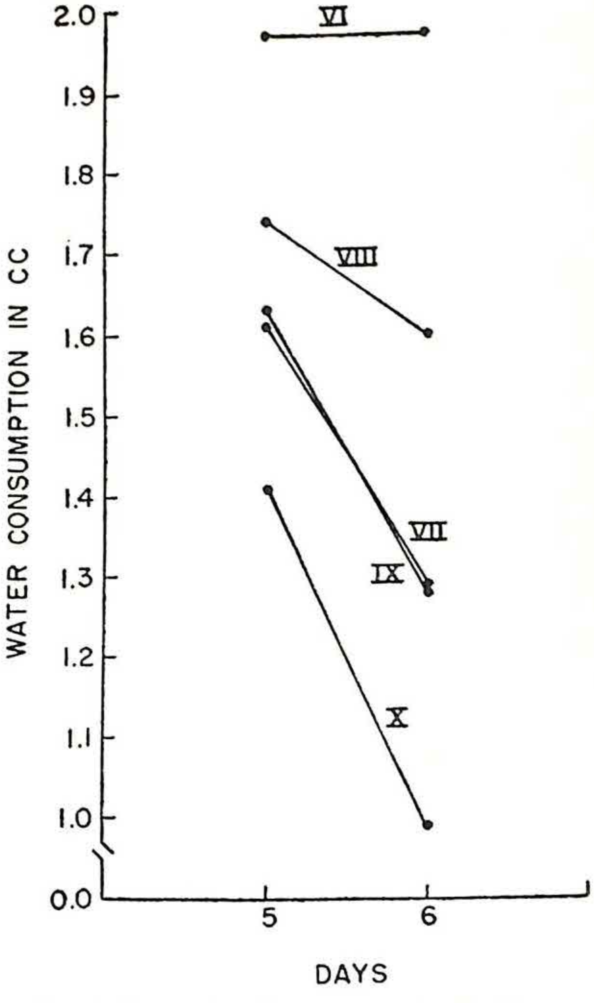

FIG. 4. Comparison of mean amounts of water consumed by groups VI to X (Set B) in first 2 min. of experimental session on days 5 and 6.

Since the means of the groups within each set showed considerable differences on day 5, the last training day, an analysis of covariance was deemed appropriate for evaluating group differences on day 6, the differential-treatmen

Two kinds of box covers, ribbed glass and sheet aluminum, were available. A pattern of fine holes was drilled in both ends of the box to provide for ventilation. Twenty such boxes were used because 20 *S*s were run simultaneously per session. The boxes were located on racks, four per rack, with a 3-ft., 30-w., daylight-type fluorescent tube providing overhead illumination for each rack.

Light, sound, and tactual conditions were presented as follows:

Light from the fluorescent fixture illuminated the box interiors when the glass covers were on, but not when the metal covers were on. A General Electric exposure meter, Type DW-68, gave readings of 56 ft.-candles for the illuminated box, and 0 ft.-candles for the darkened box.

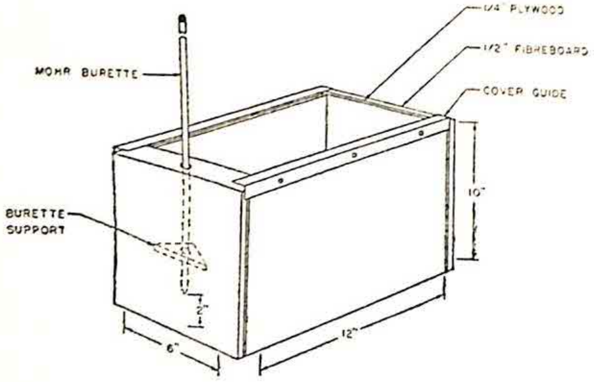

FIG. 1. Sketch of experimental box

TABLE 1

Experimental Design

SET	GROUP	DAYS 1 TO 5	DAY 6
A	I	*t s l*	*t s l*
	II	*t s l*	*T s l*
	III	*t s l*	*t S l*
	IV	*t s l*	*T S l*
	V	*t s l*	*T SL*
B	VI	*L S T*	*L S T*
	VII	*L S T*	*l S T*
	VIII	*L S T*	*L s T*
	IX	*L S T*	*l s T*
	X	*L S T*	*l s t*

To enable simultaneous use of two different sound levels for different *S*s during the same experimental hour, two experimental rooms were used. One room was sound insulated with Celotex, the other was not. The insulated room was used for low sound level, approximately 5 db.; in the noninsulated room, which was used for high sound level, approximately 85 db., a 300-cycle tone generated by a Hewlitt-Packard oscillator was presented through a loudspeaker.

Roughness of tactual conditions of the floor and walls of the boxes was effected by the presence or absence of 1/16-in. mesh wire screen. When this screen was superimposed upon the plywood floor and walls, the tactual condition was called *rough*; when the bare plywood surface was used, the tactual condition was called *smooth*.

Procedure

All *S*s prior to the experiment drank out of water cups and troughs; none had access to drinking tubes. For the five days preceding the first experimental day, *S*s were maintained on a 23-hr. water-deprivation schedule. Throughout the experiment, each *S* was run 1 hr. per day on 23-hr. water deprivation.

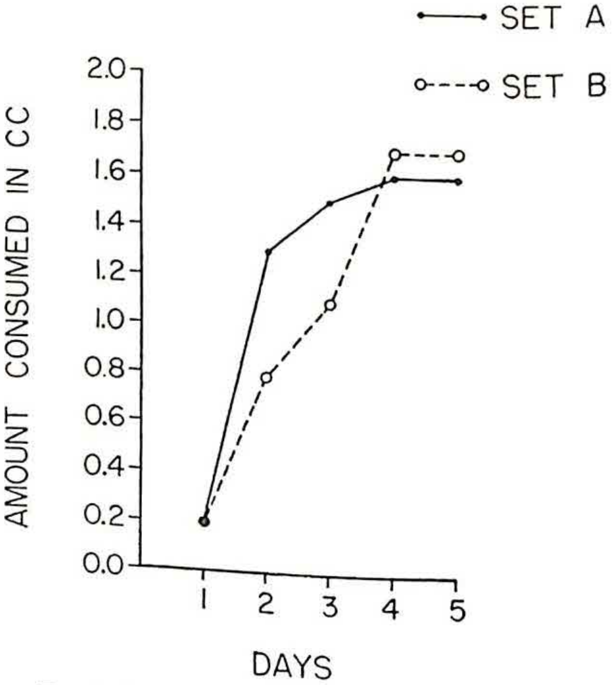

FIG. 2. Learning curve as measured by water consumption in first 2 min. on experimental days 1 to 5.

To accommodate the 100 *S*s with which the experiment was begun,[3] there were five experimental sessions per day. Two *S*s from each of the ten experimental groups were run simultaneously per session.

Table 1 indicates the plan of the experiment. The lower-case letters *t*, *s*, and *l* refer to tactual condition smooth, sound level low (5 db.), and light eliminated. The capital letters *L*, *S*, and *T* refer to light in box, sound level high, and tactual condition rough.

For each of the first five experimental days, each *S* was placed in the experimental box for 1 hr. during which time it was able to drink from the burette. For Set A animals ($N = 45$), conditions *t*, *s*, and *l* prevailed. For Set B animals ($N = 43$), conditions *L*, *S*, and *T* prevailed.

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[3] Twelve *S*s contracted pneumonia during the course of the experiment leaving a minimum of eight *S*s in a group.

day. The results of this analysis are seen in Table 2. An over-all covariance analysis for the Set A groups yielded an *F* significant at the 0.1 per cent level of confidence. A similar analysis for groups in Set B also yielded significance at the 0.1 per cent level. Significance levels for the differences between Group I and each of the other groups in Set A, and between Group VI and each of the other groups in Set B, are available in Table 2.

In general, changing the light component was most effective, changing the sound component was moderately effective, and changing the tactual component was least effective in modifying the strength of the learned drinking response. Further, the greater the number of stimulus components changed, the greater the response decrement.

TABLE 2

p-Values for Analyses of Covariance for Group Differences on Day 6

GROUPS	*p*
Set A, I to V over-all	.001
I vs. II	—
I vs. III	.05
I vs. IV	.05
I vs. V	.01
Set B, VI to X over-all	.001
VI vs. VII	.05
VI vs. VIII	—
VI vs. IX	.01
VI vs. X	.01

DISCUSSION

These results suggest that response strength is monotonically related to the proportion which conditioned stimulus events constitute of the total of stimulus events available in the immediate experimental situation.

At first blush, these results seem at odds with those of Ferster, for he reported no significant differences between *S*s for which certain stimulus components were maintained and *S*s for which those components were changed. But a comparison of his stimulus situation with ours reveals certain differences.

In our situation, a response was conditioned in the presence of continuous light and showed a significant decrement when the light was eliminated. In Ferster's situation, a response was conditioned in the presence of an intermittent light stimulus, (1 sec. on, 1 sec. off) which might be considered as an alternately light and dark situation. This situation, we suggest, may have permitted conditioning both in the presence and the absence of light inasmuch as a rat can easily perform a complete bar pressing in 1 sec. Thus, we should not be surprised if a group of *S*s trained in this way continues to show a high level of responding in a continuous no-light situation. We would go even further and suggest that had Ferster tested a group under continuous light, it would have shown similar results. It is not intended that this analysis should be applied indiscriminately to all intermittent stimuli. We should feel safe with reference to intermittent stimuli of longer intervals; but, as the duration became considerably shorter, so that an *S* could not perform a bar pressing within the interval, different effects (such as obtaining our kind of results in Ferster's kind of situation) might be expected; i.e., the flickering light would then be behaving like a homogeneous stimulus instead of a succession of discrete stimulus situations.

The sizable difference in the intensities of light used in the two experiments, 56 ft.-candles in our situation as compared with 0.01 ft.-candles in Ferster's, should not be overlooked. We may wonder whether Ferster would have obtained our results, or we his, had we exchanged intensities. From our results and our analysis of the intermittent light situation, we would expect him to get similar results at somewhat higher illumination levels. However, what added complications would be introduced relating to dark- and light-adaptation phenomena when our extremely different intensity levels were used in Ferster's intermittent-stimulus situation could be ascertained only by specific investigation.

But what if, in our experiment, we were to have used his intensity of 0.01 ft.-candles? Would we have obtained the same results? This, too, can be answered only by means of a parametric investigation utilizing various light-intensity levels. We might reasonably anticipate that response decrement would be functionally related to differences in light-intensity levels.

It should be noted, finally, that whereas we used a 300-cycle tone at 85-db. level, Ferster used a 750-cycle tone at an unstated intensity.

For Estes and Burke, response probability is a monotonic function of the relative weights of conditioned stimulus elements present in the immediate sample of stimulus elements. Let us compare this with our empirically based statement that response strength is a monotonic function of the proportion which conditioned stimulus events constitute of the total of stimulus events available in the immediate experimental situation.

Although we speak of *response strength*, it will be observed that Estes and Burke speak of *response probability*. Their formal theory construction has not yet been developed to include specific statements about rate and amplitude, although Estes (1) has a specific development with regard to response latency. Inasmuch as our measure of water consumption may be viewed as either a rate measure or an amplitude measure, we chose to speak of *response strength* as defined by our measuring technique. Further, we make the assumption that whatever the specific functions later found to maintain between the Estes-Burke response-probability concept and empirical measures, they will be of monotonic form.

Estes and Burke speak of response probability as a function of the relative weights of conditioned stimulus elements present, whereas we speak of response strength as a function of the *proportion* of conditioned stimulus events present. It is seen readily that if the relative weights of the conditioned stimulus elements are assumed equal, our statement is, in this respect, equivalent to the Estes-Burke statement. Since we have no explicit technique for assigning specific differential weights, we have made this simplifying assumption to enable a statement of what we expected to happen in our experimental situation. These expectations, as we have seen, have been confirmed.

Finally, the statement of Estes and Burke refers to *stimulus elements* whereas we refer to *stimulus events*. Since the Estes-Burke constructual stimulus elements are placed in correspondence with empirical stimulus events, it is evident that our empirically based statement and their logically derived statement are, with the limitations indicated, in correspondence.

SUMMARY

Eighty-eight albino rats learned a tube-drinking response in the presence of specified light, sound, and tactual stimulus components during a five-day training period. On day 6, when the training stimulus components were varied, significant response decrements were observed. Light changes were most effective, sound changes were moderately effective, and tactual changes were least effective in modifying the strength of the learned drinking response. Further, the greater the number of stimulus components changed, the greater the response decrement. This suggests that response strength may be monotonically related to the proportion which conditioned stimuli constitute of the total of stimuli available in the immediate experimental situation.

The relation of these results to S-R contiguity theory was discussed.

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A DEMONSTRATION OF SUPERIOR RESISTANCE TO EXTINCTION FOLLOWING CONTINUOUS REINFORCEMENT AS COMPARED WITH PARTIAL REINFORCEMENT[1]

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The purpose of the present investigation is to attempt to demonstrate superior resistance to extinction by continuous reinforcement, as compared with a partial-reinforcement procedure. It was expected that this would be accomplished by manipulating both secondary-reinforcement and stimulus-generalization variables. These two mechanisms have been invoked in an attempt to integrate the results of studies involving a partial-reinforcement procedure within a stimulus-response reinforcement theory.

Hull (3) had emphasized the influence of stimulus generalization on resistance to extinction by assuming that during acquisition under partial reinforcement, certain unique response-produced cues were evoked following nonreinforcement. These cues, in turn, would be present at the beginning of the next trial and would, therefore, tend to become connected to the instrumental response if the next trial were rewarded. This would result in developing greater resistance, for response-produced cues which had been previously conditioned to the instrumental response would be present during extinction. The continuously reinforced group, on the other hand, would be extinguished on a "generalized set of cues" because the cues produced by nonreinforcement had never been present during acquisition. Sheffield (9) tested Hull's hypothesis by comparing the resistance to extinction of partially and continuously reinforced animals following acquisition under conditions of distributed and massed training. She found that with massed training, the partially reinforced animals required significantly more trials to reach the extinction criterion than the continuously reinforced group. Such findings were consistent with previous studies (5, 6, 10) wherein partially reinforced responses were found to be considerably more resistant to extinction than responses reinforced on every trial. With distributed training, however, the difference in favor of the partially reinforced group disappeared; i.e., there was no significant difference between the extinction rates of the partially and continuously reinforced animals. Although Sheffield demonstrated the importance of distribution of practice, it should be noted that she failed to find greater resistance to extinction by continuously reinforced animals. If "stimulus generalization" is the only factor underlying the greater resistance to extinction after partial reinforcement, then presumably the elimination of this variable should produce greater resistance following continuous reinforcement.

Another factor invoked by S-R-reinforcement psychologists to describe greater resistance after partial reinforcement is that of secondary reinforcement. Denny (2) found in a T-maze study that when secondary reinforcement was allowed to operate, acquisition proceeded almost as well with partial as with continuous reinforcement. When he minimized the effects of secondary reinforcement by changing the brightness of the goal box during nonrewarded trials, he found that the continuously reinforced group learned more rapidly that did the partially reinforced group. He also found that during extinction the 100 per cent group extinguished somewhat slower (although far from being significant) than the partial group. The major implication of this T-maze study is that secondary reinforcement is an important variable in experimental procedures involving partial reinforcement.

The experimental results of Denny and Sheffield raised the question of whether significantly greater resistance to extinction could be demonstrated following continuous reinforcement as compared with partial reinforcement in a simple instrumental conditioning situation in which the effects of secondary reinforcement and stimulus generalization were effectively controlled. The purpose of this study was to explore this possibility.

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[1] This report constitutes a portion of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology of the Graduate School of Arts and Science of New York University. The writer wishes to express his gratitude to Professor Howard H. Kendler for his many helpful suggestions and criticisms offered throughout the course of this investigation. He is also indebted to Professor L. W. Crafts.

METHOD

Subjects

Nineteen naive male rats purchased from the colony of Red Bank, N. J., were used in this experiment. The age of the *S*s at the start of the experiment was 90 days.

Experimental Design

The *S*s were randomly assigned to either Group P ($N = 10$) or Group C ($N = 9$). This experimental design involved the acquisition and extinction of a panel-pushing response acquired under conditions of partial (Group P) and continuous (Group C) reinforcement. An attempt was made to minimize the secondary reinforcement received by Group P during their nonreinforced trials. This was done by rewarding Group P in a white end box and not rewarding them in a black end box. In addition to this it was also attempted to prevent the cues resulting from nonreinforcement from becoming connected to the panel-pushing response of the *S*s in Group P by having the panel-pushing response acquired under conditions of distributed practice. During extinction a gray end box was used to minimize the effects of generalization from the black and white end boxes used during acquisition.

Apparatus

The apparatus was a straight alley runway, consisting of a starting box, guillotine-type door, delay box, and a goal box. In order to manipulate the secondary reinforcement variable in this problem, three goal boxes were used; one was painted white, one black, and the last (extinction box) gray. The goal boxes were horizontally adjacent to each other and separated by plywood panel. In front of each goal box was a gray delay box. The gray starting box containing the gray guillotine door could be shifted in front of any one of the gray delay boxes, each of which had a panel arrangement at the rear of the box similar to that employed by Kimble (7). This panel was pivoted so that the animal need exert only a very light pressure in order to enter the goal box.

Raising the guillotine door a distance of 1 in. depressed a microswitch, which started a Springfield timer. Opening the panel closed another microswitch, which activated a holding relay that stopped the timer and thus recorded the latency of the response to the nearest 0.01 sec. A 75-w. GE bulb was placed directly over the food compartment used under each of the specific experimental conditions. The rest of the room was dark.

In addition to the above experimental apparatus, a similar apparatus was used for the preliminary training. The box had the same dimensions as the experimental apparatus and was of shellacked natural wood.

Procedure

Preliminary training. All *S*s were given two weeks of habituation during which a strict food regimen was maintained. Each *S* received 10 gm. of Purina Dog Chow per day at approximately the same hour as they were to be run in the experiment. During the two-week period *S*s were handled daily and fed in cardboard boxes of different shapes in different parts of the experimental room. After this period of adaptation each *S* received five massed reinforced trials in the preliminary training box. On each of these trials, *E* waited until *S*'s forepaws were in front of the guillotine door. When this correct position was assumed by *S*, the guillotine door was raised and then lowered as *S* passed through it into the preliminary delay box. As *S* approached the food compartment, *E* raised the panel by hand, permitting *S* to enter and obtain the food in the food compartment. The amount of time elapsing between the raising of the guillotine door and *S*'s pushing the panel a distance of 1 in. was recorded as the reaction latency. In the food compartment *S* was given three pellets of Chow each weighing 0.04 gm. When all *S*s of an experimental group had completed the five trials, they were fed 10 gm. of Chow each in their home cages, at least 30 min. following their removal from the preliminary training apparatus.

Training. Approximately 24 hr. after preliminary training, a training series consisting of 31 trials was begun. As previously indicated the response required of *S*s in this experiment was a panel-pushing reaction. On each training trial, *E* waited until *S*'s forepaws were facing the guillotine. When this criterion position was assumed by *S*, the door was raised by *E* and the timer was activated. The timer stopped when *S* lifted the panel door the requisite distance and entered the food compartment to obtain (or, not obtain) the food. On reinforced trials *S* received a small pellet of Purina Dog Chow weighing approximately 0.04 gm., in the appropriate food box. The food was placed behind an elevated obstacle in the food compartment. This obstacle was placed in all the compartments in the same position in order to preclude the possibility of *S*'s observing the presence or absence of food before pushing the door a distance of 1 in.

In the partial-reinforcement condition, an alternating order of reinforcement and nonreinforcement was utilized. In addition the first training trial of each day was always rewarded to insure that *S* would respond on subsequent trials that were nonrewarded. Also, the last training trial was always reinforced to make certain that *S* would respond (after 24-hr. interval) during the extinction series. This procedure necessitated the use of 31 trials for the partial-reinforcement groups and as trials were equated for all groups, the continuously reinforced group also received 31 trials. Partially reinforced animals received a total of 16 reinforced trials (52 per cent reinforcement).

Each *S* was given four trials per day for seven days. On the last day of training (day 8), each *S* received only three trials. A 40-min. intertrial interval was employed for the Ss of both groups.

Extinction. Twenty-four hours after the last acquisition trial, the extinction series was begun. The first trial was reinforced in the white food compartment in order to increase the probability of continued responding during the extinction trials. Following the reinforced trial, all the Ss were extinguished. During extinction, a gray end compartment was used instead of the white food compartment. The extinction trials had an intertrial interval of 20 sec. If S did not make the panel-pushing response during a 60-sec. interval following the raising of the guillotine door, S was removed from the apparatus and the behavior of S was recorded as "no response." The criterion for extinction was three successive trials during which S made "no response." The extinction data consist of the number of responses made before reaching the extinction criterion.

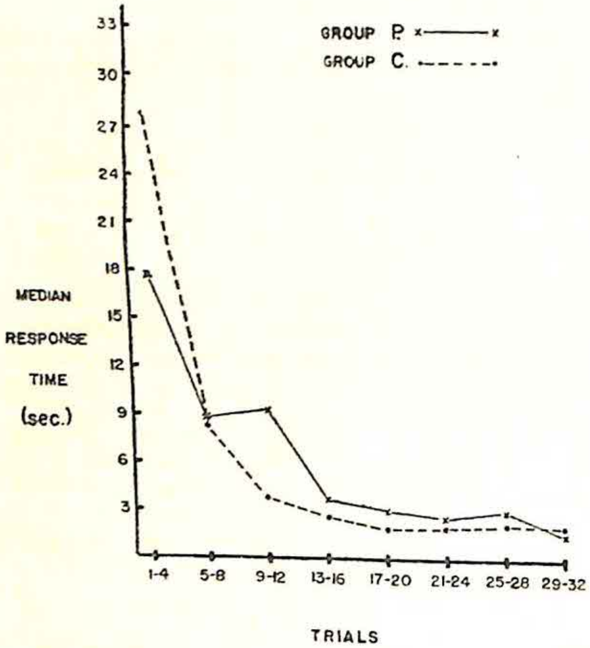

FIG. 1. Acquisition curves for Groups P and C showing median response times (averaged for successive groups of 4 trials) during 31 training trials

TABLE 1

Summary of Alexander Trend Test for the Average Log $(x + 1)$ Latency Scores Obtained during Acquisition

SOURCE OF VARIATION	df	F
Between-group means	1	5.09*
Between-group slopes	1	2.37
Group deviation from estimation	6	—
Between-individual means	17	9.72‡
Between-individual slopes	17	3.13†
Over-all deviations from linearity	6	2.96*
Over-all slope	1	235.23‡
Individual deviations from estimation (error)	102	

* Significant at the .05 confidence level.

† Significant at the .01 confidence level.

‡ Significant at the .001 confidence level.

RESULTS

Acquisition

The acquisition data were initially treated by Sheffield's method of analysis. The median latency for each S for the 31 acquisition trials was obtained. The mean of these median response times was computed for each group. A comparison of these results indicates no significant difference ($t = 0.06$, $p = .90$) between Groups C and P. There is some suggestion, however, that such an analysis may be somewhat crude, as is indicated by the latency measures graphically represented in Figure 1. The graph suggests in spite of the chance superiority of Group P over Group C for the initial four trials, a somewhat more rapid acquisition rate for Group C for the first 20 trials. It may be that the panel-pushing task is so simple that the S's "physiological limits" are rapidly reached. Because of this, the Sheffield type of analysis might fail to uncover differences occurring during the early portion of learning. This possibility was investigated by means of a trend analysis described by Alexander (1), the results of which are presented in Table 1. The log $(x + 1)$ transformation was applied to the latency data and the average value for each of the eight days for each subject was obtained. Systematic deviation from linearity is apparent in the over-all group. The significant F value obtained for "between-individual slopes" indicates that the slopes of the individual least-square straight lines are significantly different within each group. The critical term in the analysis, "between-group slopes,"

TABLE 2

Number of Responses Made by Ss of Both Groups (Group P and Group C) to Reach the Extinction Criterion

											M	Mdn.
Group P	11	10	8	7	6	5	2	1	1	1	5.2	5.5
Group C	35	27	18	15	13	12	10	10	5		16.1	13.0

is not significant. The implication is that if we fit a least-square straight line to the total body of data for the partially reinforced group, and another for the data of the group that received continuous reinforcement, then the slopes of these two straight lines would not differ significantly. Consequently, we may conclude that no significant difference in rate of acquisition existed between the partially and continuously reinforced animals.

Extinction

The number of responses made by the individual members of both groups (Group C and Group P) before the extinction criterion was realized are presented in Table 2. Because the results of Group P were highly skewed, the Mann-Whitney test (8) was employed. The result of the comparison indicates that the null hypothesis can be rejected at the 0.4 per cent level. The data indicate, therefore, that the continuously reinforced group (Group C) manifested significantly greater resistance to extinction than did the partially reinforced group (Group P).

DISCUSSION

The purpose of this experiment was to evaluate certain hypotheses proposed within the S-R-reinforcement theoretical framework about the mechanisms underlying the superiority of the partial-reinforcement procedure over continuous reinforcement as measured by resistance to extinction. It had been proposed that both stimulus generalization and secondary reinforcement were responsible for this difference. It was reasoned that if the effects of these two mechanisms, responsible for the greater resistance to extinction exhibited by partially reinforced *S*s, could be eliminated, or even reduced drastically, it might be possible to demonstrate that under such conditions continuously reinforced *S*s would take longer to extinguish than partially reinforced *S*s. Such evidence would suggest that the partial-reinforcement phenomenon is in no way inconsistent with the assumption that number of reinforcements is positively related to habit strength (4); it would merely imply that the results of partial-reinforcement studies were dependent upon factors which hid the basic relationship between learning and the number of reinforcements.

The fact that the results of the present study indicated greater resistance to extinction following continuous reinforcement under experimental conditions in which distributed practice was used and the effects of secondary reinforcement were drastically minimized for the partial-reinforcement group would tend to support our analysis of the partial-reinforcement phenomenon. There is, however, a certain precaution that should be taken in interpreting the present results. The data cannot be interpreted to be a function of the combined influence of stimulus-generalization (distribution of practice) and secondary-reinforcement variables. Inasmuch as the influence of these variables was confounded within the design, the results can be a function of either of these factors or a combination of both.

SUMMARY

The present study compared the acquisition and extinction rates of a panel-pushing response acquired under conditions of partial and continuous reinforcement. An attempt was made to minimize secondary reinforcement received by the partially reinforced group on their nonreinforced trials. This was accomplished by rewarding them in a white end box and not rewarding them in a black end box. In an attempt to prevent the cues resulting from nonreinforcement from becoming associated with the panel-pushing response of the *S*s in the partially reinforced group, the acquisition trials were distributed (40-min. intertrial interval).

The results revealed no significant difference between the response times of the partially and continuously reinforced groups during the 31 acquisition trials. The major finding of the present study was that the continuously reinforced *S*s demonstrated a greater resistance to extinction than did partially reinforced *S*s.

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EXPERIMENTAL EXTINCTION AS A FUNCTION OF THE PREVENTION OF A RESPONSE[1]

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In presenting his goal gradient hypothesis, Hull indicated that the blocking or interruption of goal-oriented responses would bring about a state of affairs akin to those produced by experimental extinction. He proposed a frustration hypothesis which states ". . . that whenever an excitatory tendency is prevented, for any reason, from evoking its accustomed reaction, a state ensues substantially like the experimental or internal inhibition long known to be characteristic of conditioned reactions" (2, p. 10).

Later, Williams and Williams (5) put this hypothesis to an experimental test. Running rats on a straight and L-shaped runway, and using the latencies of the first four extinction trials as their measure of response strength, they found latencies for those animals prevented from reaching the goal box by a barrier were significantly longer than for those animals which were permitted to enter the goal box but found no food.

The present study was an attempt to verify further and to extend Hull's frustration hypothesis and the experimental findings of Williams and Williams.

METHOD

Subjects

The subjects for the study consisted of two groups of experimentally naive albino rats, each group containing ten male and two female animals of approximately 90 days of age. These animals, of a Harlan strain, were obtained from the colony maintained by the department of psychology of The Pennsylvania State College.

Apparatus

The apparatus employed consisted of two identical wooden boxes with grid floors and hinged covers. Each box measured 15 in. by 9 in. by 12 in. Three walls and the ceilings of the boxes were painted white, and the remaining side of plate glass permitted observation of the animals. The boxes were placed end to end and connected by a vertically sliding door which was operated manually by one of the experimenters. The grid floors consisted of $\frac{1}{8}$-in. brass welding rods which were placed at $\frac{1}{2}$-in. intervals. It was possible to charge the floor of the first box with direct electric current supplied by a Variac which was wired in series with a 1500-ohm resistance.

Procedure

Learning series. Each subject was permitted 1 min. in the apparatus with the door between the chambers remaining open. The animal was then removed and placed in a retaining cage. Twenty seconds later the subject was placed in the first box. The door between the boxes remained closed for a period of 5 sec. and was then raised. Two seconds later the current was turned on, and the grid floor of the first box remained charged until the subject had escaped into the second box. The door was then closed, and 10 sec. later the animal was removed from the second box and placed in the retaining cage. Twenty seconds later the second trial was begun. This procedure was followed until the animal reached a criterion of three consecutive escapes in the 2-sec. interval occurring between the opening of the door and the application of shock.

Extinction series. Twenty seconds after the last learning trial, the extinction series was started. Time sequences were the same as in the learning series. Control animals were given regular extinction trials until they failed on three successive occasions to leave the first chamber within 10 sec. after the door had been opened.

The first five extinction trials for the experimental subjects were blocked. That is, after the animal had been placed in the first box, it was retained there for a period of 15 sec., the door remaining closed. Commencing with the sixth trial, the door was raised and the remaining trials were the same as those of the control subjects. These continued until the animal failed on three consecutive runs to leave the first chamber within 10 sec. after the raising of the door.

RESULTS

The results are relatively straightforward in indicating that those animals which were prevented from making the escape response early in the extinction series, extinguished more rapidly than the group always given the opportunity to make such a response.

Table 1 indicates that though both groups had approximately the same number of reinforcements during the learning series, the "blocked" group required a significantly smaller number of trials to reach the extinction criterion. The difference between these groups is significant between the .01 and .02 level of confidence.

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[1] This study was presented to the Division of Experimental Psychology at the 1951 meeting of the APA.

[2] Now employed at the University of Wisconsin.

CONCLUSIONS

The evidence provided by this experiment lends further support to Hull's hypothesis that response interruption results in behavior similar to that noted in experimental extinction (2). These results also appear to corroborate the findings of Williams and Williams (5) in that response prevention serves as a more effective means of producing response cessation than traditional extinction procedure.

TABLE 1

Number of Trials to Reach Learning and Extinction Criteria

GROUP	N	LEARNING		EXTINCTION		t	p
		Mean	σ	Mean	σ*		
Control	12	13.42	6.49	38.08	25.32	2.85	$<.02$
Experimental..	12	13.50	6.39	12.67	15.29		

* The difference between the extinction variances is sufficiently large to cause concern regarding their homogeneity. The t computed for this difference is between the 10 and 20 per cent level of confidence. In order to evaluate the results conservatively by compensating for the possibility of variance heterogeneity, the authors have followed the recommendation of Snedecor (4) and halved the degrees of freedom when entering the t table.

Williams and Williams (5) have accounted for their findings in terms of Hull's goal gradient hypothesis. The strength of the approach tendency in the goal gradient hypothesis is considered to be a function of the distance from the goal. Thus, blocking at a point farther from the goal would be more effective in inducing extinction than allowing the animal to reach the goal, inasmuch as the approach tendency would be weaker at the farthest point.

It would appear to the authors that two alternative explanations are perhaps more parsimonious and seem more relevant to an avoidance-learning situation. Such alternative explanations center about the presence of one or two factors which might be operating to produce the experimental findings.

The first might be described as counter-conditioning. In this instance, the experimental animals would be learning to make a new response during the blocked trials. Such a response would be learned inasmuch as it would be reinforced by the absence of shock (and pain) and the subsequent decrease in fear. Even though the door was raised later in the series, this new response of remaining in the first box would be sufficiently strong to weaken seriously or inhibit the previously learned escape response.

It is possible also that the experimental findings could be accounted for on the basis of diminished drive strength. It is generally accepted that neutral stimuli, through a process of learning, can acquire drive properties. In the present design, it is possible that the blocked trials provided the animal with an opportunity to learn that the stimulus which had acquired secondary motivating characteristics was no longer potent. Thus, without the appropriate drive being present, the escape response would not be made.

The major differences in the explanations provided are that in the first, it is posited the box remains capable of eliciting fear, but the organism has learned an appropriate response to reduce it. In the second explanation, it is posited that the previously neutral stimulus has lost its capacity to arouse the drive.

SUMMARY

The effectiveness of response interruption was investigated in an avoidance conditioning situation. Two groups of rats learned to escape from the first of two identical boxes to the other to avoid an electric shock. Control animals were then given typical extinction trials. Experimental animals were prevented from making the escape response for the first five trials, and then they were given regular extinction trials. Comparison of the groups indicates that the experimental or blocked animals extinguished significantly more rapidly than the controls.

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VARIABILITY AND REACTIVE INHIBITION IN THE MEAL WORM AS A FUNCTION OF DETERMINED TURNING SEQUENCES

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The concept of reactive inhibition offers an approach to the whole problem of variability in behavior. Rather than considering variability a function of unisolated chance factors or attributable to still unknown physiological events, reactive inhibition makes variability a lawful product of behavior itself. As stated by Lepley and Rice:

> When any reaction occurs, the probability of its later occurrence is reduced. The probability of its later occurrence increases with the continuing succession of following, dissimilar reactions. It is proposed that the probability of later occurrence would be reduced progressively with continued repetition; and that the degree of reduction would be proportional to the degree of repetitiousness. It is further proposed that this reduction in the probability of occurrence for a particular reaction would enhance the probability of occurrence for other reactions in the repertoire (3, p. 283).

Reactive inhibition and its relation to conditioned inhibition has been a fairly standard explanation for extinction in conditioning theory (1). Recently, Lepley (2) and Lepley and Rice (3) have extended the concept of reactive inhibition (I_R), as a source of variation, to such phenomena as language in man and maze behavior in the paramecium. The experiment of Lepley and Rice applies the concept to the simple-choice turning of paramecia following a forced-choice turn. The present study attempts to retest the original deductions, namely, that after a forced-choice turn, the organism will turn in the opposite direction at the next choice point. In addition, an extension of the basic proposition is offered. This proposition is suggested by them (3) and inherent in the whole concept of reactive inhibition, namely, that reactive inhibition is a transitory effect and is dissipated with time or distance (depending on the nature of the interpolated activity). The first three conditions of this experiment are similar to those of the paramecium study.

1. When an animal approaches a T choice point along a path without turns, the probability of its turning right or left will approximate chance expectation.

2. When an animal approaches a T choice point along a path requiring one preceding right (left) turn, the probability of its turning in the opposite direction will be increased.

3. When an animal approaches a T choice point along a path requiring two preceding right (left) turns, the probability of its turning in the opposite direction will be greater than that following a single preceding right (left) turn.

The paramecium study supported the first two deductions only. A decrease in opposite turning was found for condition 3. In order to account for this, it was suggested by the authors that a possible distribution of the animal's activity, in time, may occur, i.e., a longer swimming time on the second pathway. As a result, reactive inhibition, or some portion of it, is dissipated with a consequent decrease in opposite-turning behavior. To test this proposition, a fourth condition was added to the previous ones:

4. When an animal approaches a T choice point along a path requiring one preceding right (left) turn, the probability of turning in the opposite direction is related to the distance between the first turn and the choice point; the longer the distance, the closer the turning behavior will approach a 50:50 expectation.

METHOD

Subjects

The subjects of this experiment were approximately 800 meal worms, larvae of *Tenebrio molitor*. The larvae measured from 2.3 cm. to 2.7 cm. in length. Their width varied from 3.0 mm. to 3.4 mm. This species, rather than one of paramecia, was selected for two major reasons. First, it is difficult to etch mazes of the size appropriate to paramecia without marked irregularities in the pathways. Secondly, the meal worm represents a higher order in the phylogenetic scale and affords a comparative study of reactive inhibition between the meal worm and the paramecium. In addition, because of the size and activity of meal worms, runs involving only one organism are possible.

Apparatus

The 11 mazes were made of plaster of Paris, from molds with 4-mm. glass tubing as the imprint source, and covered with equal proportions of beeswax and paraffin. Before the coating, each maze was carefully sanded to remove any irregularities in the pathways and the choice points. Each maze consisted of a starting well, connecting pathways of various lengths, a number of forced turns, and a choice point. The five major experimental variants were as follows:

1. T: a maze with a 3-cm. pathway and no turns between the starting well and choice point.
2. R-T: mazes with pathways of 1½, 3, 6, and 12 cm., respectively, between forced right turn and choice point.
3. L-T: mazes with pathways of 1½, 3, 6, and 12 cm., respectively, between forced left turn and choice point.
4. R-R-T: maze with two 3-cm. pathways between *two* forced right turns and choice point.
5. L-L-T: maze with two 3-cm. pathways between *two* forced left turns and choice point.

Procedure

Because of practical considerations, a sample-size of 50 subjects was deemed adequate for each of the forced-turn mazes, for the results combined according to prediction would result in an N of 100 for each length. The sample-size for the T maze was 100. In addition, as a pretest for biasing factors in each maze (except T), a sample of 20 subjects was employed. Therefore, a total of 700 meal worms was actually used.

The meal worms were maintained in a growth mash and were sifted from it about a half-hour before the actual run in order to insure lively activity. Any larvae showing signs of metamorphosis, sloughing of skin, or general lethargy were discarded at once. Each maze was placed on an 8-in. square platform and centered and *leveled* on a table tripod. This insured against any biasing effect of gravity in determining turns. The standard procedure and rules for the single run that each worm made were as follows: the animal was placed in the starting well, and a clear plastic cover was placed over the entire maze. Any animal that did not start into the pathway immediately, or after one gentle tapping of the maze, was discarded. During the run, any animal that tended to "creep," back up, take more than 5 sec. to make a choice at the choice point, or crawl along the side instead of moving down the center of the pathway, was discarded. As soon as an animal was discarded, a new one was started until 50 animals had been run for each condition. All the above criteria resulted in the rejection of from 80 to 100 animals, and the last condition was responsible for approximately 75 per cent of the total discards.

RESULTS AND INTERPRETATIONS

The first proposition to be tested was that for an animal approaching a T choice point along a path without turns, the probability of its turning right or left would approximate chance. Actually, 52 per cent of the animals turned left and 48 per cent turned right. This difference of 4 per cent is well within chance variation and clearly supports the first proposition.

Since the remaining propositions support a preferential turning, it is essential that such turning preference be a product of the previous behavior, not of bias in the maze. In order to rule out any such bias, 20 meal worms with no previous turning experience were run in each maze. They were placed in the alleyway before the choice point.[1] The results of this pretest (Table 1) indicate very close approximation to a 50:50 choice for all mazes at the choice point.[2]

TABLE 1
Distribution of Turns in Pretest of the Mazes

DIRECTION OF TURN	MAZE LENGTH IN CENTIMETERS									
	1½		3		6		12		(2) 3	
	L-T	R-T	L-T	R-T	L-T	R-T	L-T	R-T	L-L-T	R-R-T
Left	10	9	9	9	10	11	11	10	11	10
Right	10	11	11	11	10	9	9	10	9	10

TABLE 2
Comparison of Length and Right- and Left-Turning Mazes: Analysis of Variance

	df	SUM OF SQUARES	VARIANCE
Right and left mazes...	1	8.1	8.1
Length............	4	357.0	89.3*
Remainder (M × L)...	4	19.4	4.9
Total.............	9	384.5	

* F equals 18.22 for 4 and 4 df. F of 15.98 needed at the .01 level.

In the experiment proper, the major hypotheses are verified. When an animal approaches a T choice point along a path requiring one preceding right or left turn, the probability of its turning in the opposite direction is related to the distance between the forced turn and the choice point. An analysis of variance (Table 2) of the turning behavior indicates clearly that length of pathway is a highly significant variable, but there is no significant difference between the right and left forced-turn mazes. For the combined results of R-T and L-T mazes of 1½ cm., 85 per cent turned in the predicted direction (i.e., opposite to the previous forced turn). The percentage decreases as the distance between the forced turn and choice point increases, and approaches 50 per cent at 12 cm. The differences for 1½, 3, and 6 cm. when tested against a 50:50 expectation, are significant beyond the .01 level of confidence (Table 3). The analysis of the R-T and L-T mazes separately gives the same general picture, with equivalent magnitude of significance for each length of maze. The results support the hypothesis and previous findings that reactive inhibition from a specific response is dissipated in time. Therefore, other things being equal, the shorter the time after the evocation of a response, the greater is the probability that a subsequent response will differ from the previous one.

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[1] Since the meal worm is longer than the 1½-cm. alleyway of the shortest maze, a metal sleeve extended the alleyway over the forced turn.

[2] It was decided prior to this test, that any maze resulting in a division greater than 11:9 would be discarded.

TABLE 3

Percentage Turning in Predicted Direction for Control, One-Turn, and Two-Turn Mazes

MAZE	N	% TURNING IN PREDICTED DIRECTION	$\sigma\%$	$\frac{\% - 50}{\sigma\ \%}$
T.	100	52	4.99	0.40
One-turn				
1½ cm. . . .	100	85	3.57	9.80
3 cm.	100	84	3.67	9.26
6 cm.	100	75	4.33	5.77
12 cm.	100	58	4.94	1.62
Two-turn				
3 cm.	100	93	2.55	16.86

When an animal approaches a choice point along a path requiring two preceding right or left turns, the probability of turning in the opposite direction will be even greater than the probability following one turn. This proposition was not supported by the Lepley and Rice study, but is borne out by the data from the 3-cm. L-L-T and R-R-T mazes of this experiment. The combined results show that 93 per cent of the animals turned in the direction opposite that of the two preceding forced turns. This is a greater percentage than found for even the 1½-cm. single-turn maze, and this difference is significant between the .06 and .07 levels. When the double-turn maze is compared with the single-turn maze having alleyways of comparable length, i.e., 3 cm., the difference is significant at the .04 level of confidence. To account for their failure to find this support, Lepley and Rice offered two hypotheses: (*a*) The second turn establishes a habit strength sufficient to negate partially the reactive inhibition of the repetitive behavior; and (*b*) The distribution of the animals' activities, in time, between turns may permit partial recovery from reactive inhibition and thereby decrease the probability of opposite-turning behavior.

The results of this study on distance and reactive inhibition clearly support the latter hypothesis as a feasible explanation for their failure. It is then possible that the time required for the paramecium to swim the second leg of the maze was longer than for the first, allowing some dissipation of reactive inhibition and thereby decreasing opposite-turning behavior. It is conceivable as well, and thereby producing the same over-all effect, that for the paramecium, the length of pathway between turns was sufficiently long to dissipate some of the reactive inhibition, and shorter pathways would have demonstrated the effect.

SUMMARY

The experiment reported was designed to retest the original hypotheses of Lepley and Rice regarding reactive inhibition in maze-turning behavior, using meal worms instead of paramecia. Fifty meal worms were employed in each of 11 mazes. The control maze consisted of a straight pathway followed by a T choice point. Eight mazes consisted of a single forced turn with pathways of varying lengths following the forced turn and preceding the choice point. In addition, two mazes had two forced turns preceding the choice point. The distribution of right and left turns in the control maze closely approximated chance frequency. In the one-turn mazes, the tendency to turn in the opposite direction from the forced turn was highly significant, but decreased in magnitude and significance as the

length of pathway increased. This finding is interpreted as conforming to the expectation that reactive inhibition is dissipated with time (distance). In the two-turn mazes, in contrast to the paramecium study, the turning behavior was more marked than for the shortest single-turn maze. Tentative explanations for this failure in the paramecium study are offered.

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SENSORY PRECONDITIONING UNDER TWO DEGREES OF DEPRIVATION[1]

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In an earlier study by the present author (1) four groups of rats were given sensory preconditioning training to a buzzer and a light under different degrees of food and water deprivation. The animals were later taught avoidance responses to the buzzer and the light by pairing each of these stimuli with electric shock. It turned out that those animals which had experienced sensory preconditioning under higher degrees of deprivation learned both avoidance responses faster than the animals which had been given the training under lower deprivation. Because no reward was given during the training, these results were interpreted to mean that learning during sensory preconditioning is influenced by the degree of deprivation and that this relationship is independent of reward.

However, the above interpretation of the results was open to question for several reasons. The most important criticism of this interpretation is based upon the fact that the higher deprivation groups learned not only the avoidance response to the light faster, but also the avoidance response to the buzzer. If the animals had learned an association between buzzer and light during the training, this would be expected to influence the rate at which an avoidance response could be transferred from the buzzer to the light, but not the rate at which an avoidance response is learned to the buzzer in the first place. The performance of a control group in the above study indicated that the faster rate of learning the avoidance response to the buzzer was probably the result of a higher activity level. The animals that had experienced sensory preconditioning under higher deprivation had been deprived for ten days, and after-effects of this prolonged deprivation apparently caused a higher activity level during the learning of the avoidance response to the buzzer.

The present experiment was designed to eliminate differences in the activity level of the animals after the sensory preconditioning training is completed. The design of this study was also changed in such a way that sensory preconditioning could be demonstrated more easily.

One reason for the difficulty of demonstrating the effects of sensory preconditioning in rats is the amount of time which usually elapses during such an experiment. Sensory preconditioning studies which follow the original design of Brogden (2) usually are arranged in three parts. The subjects are first stimulated simultaneously by two neutral stimuli (e.g., a light and a tone) a number of times. In the second part, one of the two stimuli is used as a conditioned stimulus for some response, and in the third part, the second of the two stimuli is presented to test whether the conditioned response is transferred, thus giving evidence of learning during the first part of the experiment.

Because the learning during sensory preconditioning does not become apparent until the third part of the experiment, the animals have a chance to forget the original learning during the second part. In order to minimize this possibility, the second part should be as short as possible. The present experiment accomplishes this by using a very simple avoidance response, and by continuing in the experiment only those animals that have learned this avoidance response within two days of training.

METHOD

Subjects

The subjects were 39 naive, male albino rats of the stock maintained by the Ohio State University psychological laboratories. The animals were between 90 and 140 days old at the beginning of the experiment.

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[1] This experiment was performed in the psychological laboratory of the Ohio Wesleyan University. The following students assisted in the construction of apparatus and collection of data: Adelbert Bramley, Hurley Butler, Everet Crawford, Ronald Mayer.

Apparatus

The apparatus consisted of a circular grill enclosed by an inner and outer wall of transparent Plexiglas, with diameters of 24 and 32 in., respectively. A similar apparatus was used by Hunter (4), and is also shown by Mowrer (5, p. 66). In the center of the apparatus a 100-w. light and a 6-v. buzzer were mounted. The buzzer and light were connected to an automatic timer, which turned them on simultaneously for a 2-sec. period at intervals of 30 sec. The buzzer and light could also be turned on individually by means of manually operated push buttons. The entire circular grill could be electrified by a current of 60 cycles and 750 v., with a 3,000,000-ohm resistor permanently arranged in series with the resistance of the animals on the grid. This current could be controlled manually by means of a push button, or automatically, following 2 sec. after the light or buzzer, and lasting until manually interrupted.

Procedure in Part 1

The animals were randomly divided into two experimental groups and one control group. The two experimental groups differed in the deprivation conditions established during part one. Although both groups were given food and water for 8 hr. during each 24-hr. period, they differed in their deprivation state at the time of training. Group 1 was trained after 14 hr. of food and water deprivation, and group 2 was trained immediately after food and water satiation. The control group was also trained after 14 hr. of deprivation, and was also fed for 8 hr. during each 24-hr. period.

Both experimental groups were trained by selecting six animals at random and placing them simultaneously in the apparatus. They were then presented with 60 paired stimulations of buzzer and light. Each presentation lasted 2 sec., and the presentation occurred at 30-sec. intervals. At the end of the training the animals were placed in separate deprivation cages. Group 1 was left in the deprivation cage for 1 hr. and was then placed in the feeding cage, while group 2 remained on deprivation for 15 hr. The control group differed from group 1 only in that a light but no buzzer was presented during the pretraining. The training for all groups continued for six days. At that time 360 stimulus presentations had been administered.

Procedure in Part 2

All animals were satiated at the end of sensory preconditioning and except for the experimental session were left in their feeding cages throughout the remainder of the experiment.

The animals were placed individually in the apparatus and were conditioned to run on the grid in either direction at the sound of the buzzer. The buzzer was presented at 30-sec. intervals, and if the animal failed to perform the conditioned response, a shock followed after 2 sec. Both shock and buzzer continued together until the animal had run a distance of at least 6 in., at which time the experimenter terminated both buzzer and shock. The responses of the animals were usually quite definite, and the judgment of a correct response was not difficult. Training was administered at the rate of 30 trials per day, for a maximum of two days, or until the criterion of training had been reached. The criterion was set at four consecutive correct avoidance responses. Animals which had not reached the criterion within 60 trials were eliminated. All three groups received the same training in parts 2 and 3 of the experiment.

Procedure in Part 3

The training in part 3 was the same as that in part 2, with the only exception that the light was used as the conditioned stimulus instead of the buzzer. Animals were started on part 3 on the day after they had reached the criterion in part 2. The criterion in part 3 was again set at four consecutive correct avoidance responses, and training was continued for a maximum of three days at the rate of 30 trials per day. Animals were trained in all parts of the experiment until a total of ten animals from each group had passed the criterion in part 3. It was necessary to train 39 animals in order to accomplish this. Five animals were eliminated because they failed to reach the criterion in part 2 within 60 trials, and four other animals failed to reach the criterion in part 3 within 90 trials.

TABLE 1

Means and *SD*'s of the Three Groups During Conditioning to the Light and to the Buzzer

GROUP	*N*	MEAN TRIALS TO BUZZER	*SD*	MEAN TRIALS TO LIGHT	*SD*
1 (high deprivation)	10	33.2	3.4	34.0	6.4
2 (low deprivation)	10	30.2	3.8	54.5	6.1
3 (control)	10	37.0	3.3	52.8	5.9

RESULTS AND DISCUSSION

Table 1 presents the mean number of trials required to condition the three groups to the buzzer and to the light. The differences between the group means are not significant for part 2 (training to the buzzer). In part 3 (training to the light) the means of group 2 and 3 both differ significantly at the .05 level from the mean of group 1.

The table further shows that the mean number of trials required to establish the CR to the light is greater for each group than the trials required to establish the same CR to the buzzer. Inasmuch as training to the buzzer preceded training to the light, the data appear to present a paradox inasmuch as they indicate negative transfer in a situation which all learning theories would agree to be ideal for the demonstration of positive transfer. Furthermore, since the phenomenon of sensory preconditioning rests upon the assumption of positive transfer from part 2 to part 3 of the experiment, this paradox must be resolved before the results of part 3 can be interpreted as establishing the occurrence of sensory preconditioning in this experiment.

Data from a pilot study offer a possible explanation for the apparent absence of positive transfer. These data indicate that positive transfer did take place, however, from a simple to a more difficult S-R connection. Although the response of running is the same in both cases, it appears that this response is attached more readily to the buzzer than to the light used in the experiment. In some cases the running response occurred almost as an unconditioned response to the buzzer, but never to the light. For six animals used in the pilot study a mean of 68 trials was required to learn the CR to the light, if no prior training had been given. The greater ease of attaching the response to the buzzer may be due to differences in the intensity of the light and the buzzer, or it may be due to differences in native behavior tendencies of the animals. Such differences would become particularly important in regulating the rate of acquisition of the CR when the required response is as simple as the one used in this experiment. Observations from the pilot study would therefore indicate that positive transfer did occur from part 2 to part 3, but that this transfer is not readily apparent because it only served to reduce the greater difficulty of learning the running response to the light.

In order to establish this interpretation it would be necessary to have available the record of another control group which is trained in part 1 and part 3, but not in part 2. No such control group was trained because the experimenter overestimated the amount of positive transfer which would occur. This leaves the above interpretation the most likely one, in the opinion of the writer, but does not establish it experimentally.

If we accept the above interpretation, it would follow that sensory preconditioning did occur during the experiment and that the amount of sensory preconditioning was greater for the group which experienced higher deprivation at the time of training in part 1. Furthermore, the training apparently resulted in more than a simple habituation to the light, for the control group which had only been presented with the light was not equally able to transfer the avoidance response from the buzzer to the light. The experiment therefore confirms the conclusion of the earlier study, that learning in the absence of reward is increased by the degree of deprivation. This relation is opposite to the one indicated by the results of other latent-learning studies. The results of other studies led Hilgard (3, p. 286) to conclude that latent learning could be obtained only under low degrees of motivation. In the writer's opinion this apparent conflict is best resolved by reference to a basic difference between the present and earlier studies. In the present experiment no reward was offered during the sensory preconditioning training, while a reward was usually given in those latent-learning studies which have shown the opposite relation between latent learning and deprivation. It is apparently only the combination of a strong goal demand with strong reward expectation which so restricts the perceptual activity of the animal that irrelevant cognitions cannot be formed.

The possibility of explaining the results of this study on the basis of differential secondary reinforcements derived from feeding subsequent to sensory preconditioning training is not feasible in the opinion of the writer. The animals were not fed until at least 1 hr. after this training was completed, and were also placed in separate deprivation cages at the end of each training session.

The results of this experiment are not in conflict with the results of a recent study by Wickens and Briggs (6). In this study sensory preconditioning was explained on the basis of mediated stimulus generalization. It is possible that the animals in the present experiment learned to make the same movements to the buzzer and the light during sensory preconditioning, and this association could have mediated the transfer of the CR from the buzzer to the light.

SUMMARY

Thirty-nine albino rats were divided into three groups and were trained in a sensory

preconditioning experiment. During part 1 of the experiment the animals were exposed to 360 paired presentations of a buzzer and a light; during part 2 the animals were taught a running response to the buzzer by pairing the buzzer with shock, and during part 3 the animals were taught the same running response to the light. Two of the groups were experimental groups which differed in the degree of food and water deprivation they experienced during the training in part 1. The third group was a control group which was presented with only a light, but no buzzer during part 1.

The results indicate the learning of the avoidance response to the light was facilitated by a high deprivation condition during part 1. The group which experienced higher deprivation during sensory preconditioning learned the avoidance response to the light significantly faster than the group which was satiate at the time of this training.

The occurrence of sensory preconditioning is also indicated from the performance of the control group, which received high deprivation during part 1 but was presented only with a light. This group learned the avoidance response to the light significantly slower than the experimental group which had been presented with both a buzzer and a light and which had experienced the same deprivation during part 1.

The results show that learning of the avoidance response to the light was generally slower than learning the same response to the buzzer. Since training to the light followed training to the buzzer, this indicates negative transfer, and such transfer would conflict with a sensory preconditioning interpretation of the results. In the writer's opinion the transfer from buzzer to light was positive but only appears to be negative because of the greater difficulty of learning the response to the light. This interpretation is supported by data from a pilot study but would require the records of another control group to be experimentally established.

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AN EVALUATION OF DEFECATION AND URINATION AS MEASURES OF FEARFULNESS[1]

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As any comparative psychologist knows, rats can defecate and urinate at most inopportune moments, and to trust one's judgment concerning the course of the eliminative urge in the rat is at best a risky business. For this reason, special significance attaches to conditions under which it is possible to state with some confidence the likelihood that the animal will eliminate. Unfamiliar surroundings constitute one such condition. When a rat is introduced into a strange situation, it characteristically explores, urinates, and defecates. On repeated exposures to the same situation, however, elimination diminishes steadily; it is the trial-to-trial decrease in elimination that distinguishes this *emotional elimination* (2) from the normal, unpredictable variety.

Rats are varyingly susceptible to emotional elimination. This susceptibility can be reliably measured by Hall's open-field test (2). Furthermore, it is possible through selective breeding to produce "high-elimination" and "low-elimination" strains (3). All this shows that susceptibility to emotional elimination is a meaningful dimension of behavior. But, is emotional elimination related to any other psychologically significant variables? Hall thinks it is very closely related to fear. In one of his early studies (2) he found a high correlation (.82) between frequency of elimination and failure of eating, both being measured concurrently in the open-field situation. More recently, Hall (5) has argued that failure of eating in hungry rats results from fear of the strange situation, and that, in view of the high correlation referred to above, emotional elimination could be considered as a generally valid measure, or "a standard test" (5, p. 370) of fearfulness.

It should be pointed out that the generality to other situations of the relation that Hall discovered in his validation study is not to be taken for granted. Rather, to establish the general validity of emotional elimination as a measure of fearfulness, one would have to demonstrate that the same relation holds in at least a few other situations.

PROBLEM

We shall assume with Hall that when a hungry rat is placed in a strange situation, its failure to eat is due to the arousal of a central emotional state of fear. The purpose of this study is to test the validity of emotional elimination as a measure of fearfulness in a situation other than, but similar to, the open field. Since a close relation between elimination and timidity (as measured by Stone's "stove-pipe test," for example) has also been suggested (5), it was decided to run the animals on a test of timidity as well.

PROCEDURE

Thirty-two rats (9 males, 23 females) were used in this study; 19 were albino, the rest hooded. They were approximately 100 days old at the time of testing. Each *S* was tested first in a modified open-field situation, and then, after a rest period of about a week, in a situation designed to measure timidity. Throughout the course of the experiment *S*s were kept on a deprivation schedule and were given access to food for only ½ hr. each day.

The Modified Open-Field Test

A large, floorless metal box, 24 in. by 18 in. by 16 in., was placed on a washable surface in a well-lighted experimental room. In the center of the cage was an immovable dish containing Purina wet mash. One at a time, each hungry rat was introduced into the cage, the door closed, and records taken of defecation, urination, and time spent eating for ten daily trials. Each trial lasted 10 min.; at the end of this period *S* was removed from the cage, the cage was lifted, and the glass floor washed to clear away any signs of urine and feces. On the tenth day, a metronome (approximately 150 beats per minute) was placed outside the cage just as *S* was put into it. The metronome ticked throughout the 10-min. trial, and seemed to be effective in producing fear in the animals.

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[1] This research was supported by the National Research Council of Canada.

[2] The authors are indebted to Messrs. M. P. Hyatt, M. Ripsman, L. M. Solomon, and E. B. Van Zalg for their valuable assistance in carrying out the experiment.

Timidity Test

The test of timidity was similar to one used by one of the present authors (1) in studying hoarding. Each *S* was put in a separate living cage three days prior to the timidity test. On the day of the test, the cage, with the hungry animal, was placed at the end of a 5 in. by 50-in.-wooden runner, which rested at each end on a 3-ft.-high support. The distance between the foot of the cage and the far end of the runner was 36 in. The test started when the door of the cage was opened, thus allowing *S* to wander out on the runner. The time that it took *S* to reach the food end of the runner was recorded, and was taken to be a measure of the rat's timidity. (This test was repeated on the following day in order to obtain test-retest reliability.)

Weighing

After the timidity test the *S*s were placed on a free-feeding schedule. Three weeks after resumption of normal diet *S*s were weighed. (These data are available on only 24 of the 32 rats.)

RESULTS

The results are discussed in terms of the following measures obtained from each *S*. (*a*) *Emotional elimination:* number of days on which *S* defecated *or* urinated in the modified open-field test. (Maximum score = 10.) (*b*) *Fearfulness:* time spent in eating food during the first exposures to the open field. (Maximum score = 600 sec.) (*c*) *Timidity:* time taken by *S* to emerge from its cage and reach the food at the end of the runway. If *S* did not leave the cage within 35 min., the test was terminated, and *S* was given an arbitrary score of 2,000 sec. If *S* put its two front paws outside the cage, but did not actually leave the cage, it was given a score of 1,800 sec. Test-retest reliability for the test of timidity, obtained by correlating the scores on the first day with scores on the second, was .77. (*d*) *Weight.*

It should be noticed that the measure of fearfulness is the time spent eating on the *first* trial only. The reason for not considering time scores for the following nine trials lies in the assumption that it is only on the first day that differences in time spent eating are likely to be *maximally* a function of fearfulness; on subsequent trials eating is likely to depend increasingly on other factors, such as weight, eating habits, etc. of the animal. This assumption is supported by the coefficients of correlation between weight on the one hand and time spent eating on each of the ten trials on the other. These correlation coefficients are presented in Table 1. It is seen that whereas the time scores are related to weight on Trials 2 to 9, the coefficients of correlation approach zero on Trials 1 and 10. (It will be recalled that on the tenth test a metronome was used to produce fear in the *S*s.) These results are consistent with the assumption that it is on the first day that differences in eating most truly represent differences in fearfulness.

So far as the timidity test is concerned, three *S*s obtained a timidity score of 2,000 and two of 1,800. The scores of the remaining *S*s ranged between 11 and 1563 sec., with a median of 354.

Intercorrelations (rank order) among the three variables, emotional elimination, fearfulness, and timidity, are presented in Table 2. It is obvious that there is no significant relation between fearfulness and elimination, as these traits were measured in our experiment. Nor do we find any significant relation between emotional elimination and timidity, or between timidity and fearfulness.

TABLE 1

Coefficients of Rank-Order Correlation between Weight and Time Spent Eating on Each of the 10 Trials, *N* = 24

	TRIALS									
	1	2	3	4	5	6	7	8	9	10
Weight	.17	.54	.43	.33	.55	.43	.23	.42	.41	.05

TABLE 2

Coefficients of Rank-Order Correlation among the Three Measures, *N* = 32

MEASURE	A	B	C
A. Emotional elimination....	—	−.06	−.26
B. Fearfulness.............		—	.26
C. Timidity................			—

DISCUSSION

The results show that when tests other than, but similar to, the ones used by Hall are employed for determining the relation between emotional elimination and fearfulness, no significant relation between the two is shown. This fact would argue against Hall's contention that emotional elimination can be used as a standard test of fearfulness. Emotional elimination is not a generally valid instrument for measuring fearfulness.

Of course, our conclusion does not invalidate the finding that it is possible to breed "high-elimination" and "low-elimination" strains of rats. But calling these strains "more fearful" and "less fearful," or "more timid" and "less timid," would certainly be inconsistent with our conclusion. The characteristic that is differentially bred in these strains is not fearfulness or timidity, but probably what may be best termed as autonomic reactivity, or proneness to autonomic involvement, or even susceptibility to a very general type of emotional disturbance, which leads to defecation and urination under conditions of any unusual stimulation. There is no reason for not accepting Hall's term *emotionality* to describe this characteristic so long as one recognizes that emotionality is not be be equated with fearfulness or timidity, and that it may have very little to do with what is normally called emotion or emotional behavior.

In his chapter on "Individual Differences" in Stone's *Comparative Psychology*, Hall lists a number of traits (e.g., active, aggressive, persevering) with which fearfulness is supposedly related (5, p. 378). Since it appears that in all these studies the distinction between fearless and fearful rats was based on their susceptibility to emotional elimination, none of these conclusions can be considered established in view of our findings.

SUMMARY

The purpose of the present experiment was to examine Hall's suggestion that emotional elimination (defecation and urination in a strange situation) is a generally valid measure of fearfulness. Thirty-two *S*s were given two tests from which three measures were obtained for each *S*: (*a*) emotional elimination (modified open-field), (*b*) fearfulness (failure to eat when hungry), and (*c*) timidity (modified cage-emergence test). Coefficients of correlation among these measures were not significantly different from zero. The discrepancy between these results and those of Hall (2) is discussed, and it is concluded that emotional elimination is not a generally valid measure of fearfulness.

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SHYNESS AS A FACTOR INFLUENCING HOARDING IN RATS

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In a paper on hoarding, Bindra (1) proposed an extension of the *security hypothesis* offered some time earlier by Miller and Viek (2). In his discussion Bindra made the following statement: "Hoarding depends on the difference in security offered by the cage and the alley, which in turn depends, in part, on the shyness of the individual rat" (1, p. 401). While Bindra demonstrated that there was a difference in the amount of hoarding under the two conditions used, open and closed hoarding, he merely suggested that there might be variation in the amount of hoarding due to differences in shyness. The explanation he offered is that "the more shy animals feel insecure and hoard; the less shy animals feel secure and do not hoard" (1, p. 401).

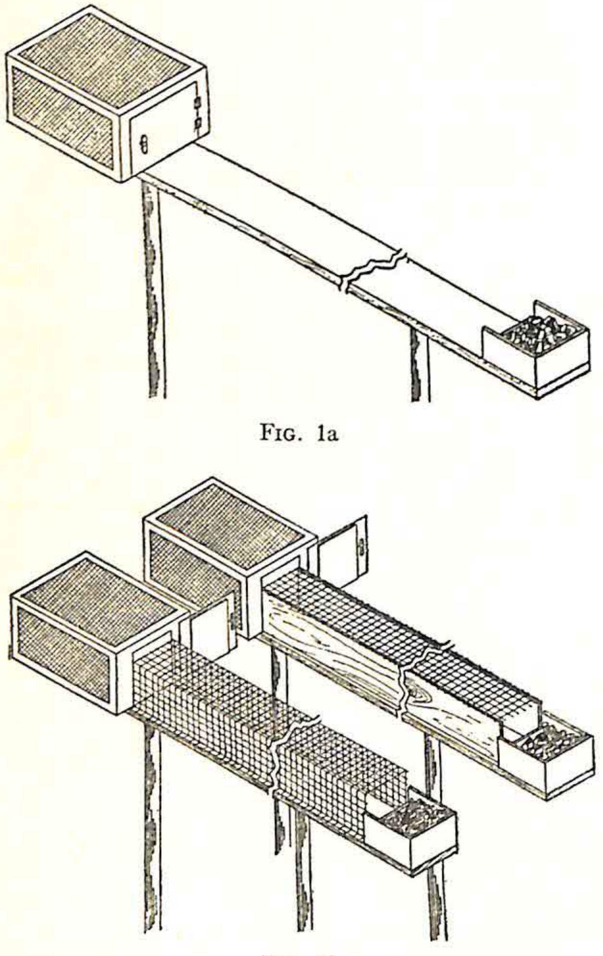

FIG. 1a

FIG. 1b

FIG. 1. Diagram of "open" hoarding alley and modifications of alley

It was decided to test this "shyness" hypothesis experimentally by means of procedures similar to those used by Bindra.

MATERIALS AND METHODS

Apparatus

The basic alley used in this experiment was a board 7 ft. long. This was supported by iron pipe at a height of about 4 ft. The boards were 6 in. wide, with the home cage situated at one end, and a food bin, 6 by 6 by 2 in., situated at the other end. A diagram of the hoarding alleys used is seen in Figure 1.

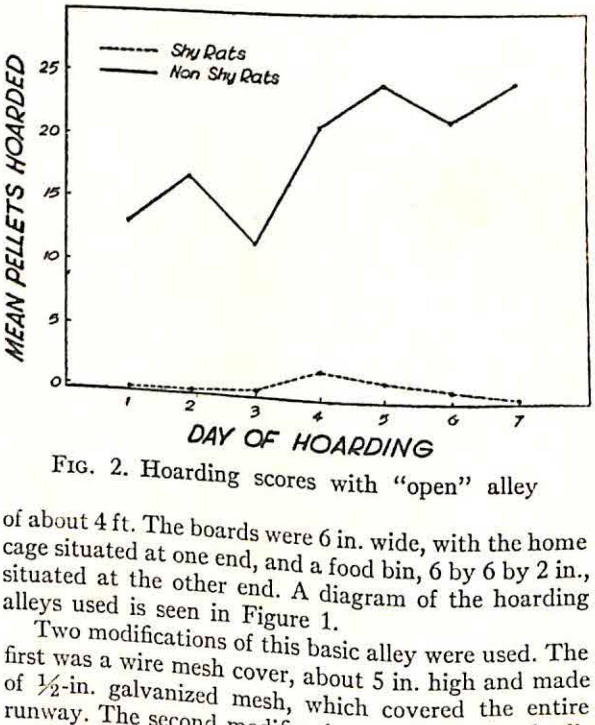

FIG. 2. Hoarding scores with "open" alley

Two modifications of this basic alley were used. The first was a wire mesh cover, about 5 in. high and made of ½-in. galvanized mesh, which covered the entire runway. The second modification consisted of a duplication of the usual hoarding alley (see 3) which could be fitted into the runway proper so that there was now a closed-type runway where there had previously been the open situation. Both modifications may also be seen in Figure 1.

Animals

Twelve male hooded rats, from a total of 27, were chosen by the method outlined in the procedure. The *S*s were about four months old, and all of them were experimentally naive.

Procedure

Shyness of all *S*s was tested by the same method as that used by Bindra as a measure of security. The length of time taken to move from the cage on to the open runway with all four feet was taken as an indication of *S*'s shyness. The *S*s which ventured onto the runway in less than 5 min. were considered to be nonshy; those that took more than 20 min. were considered to be shy.

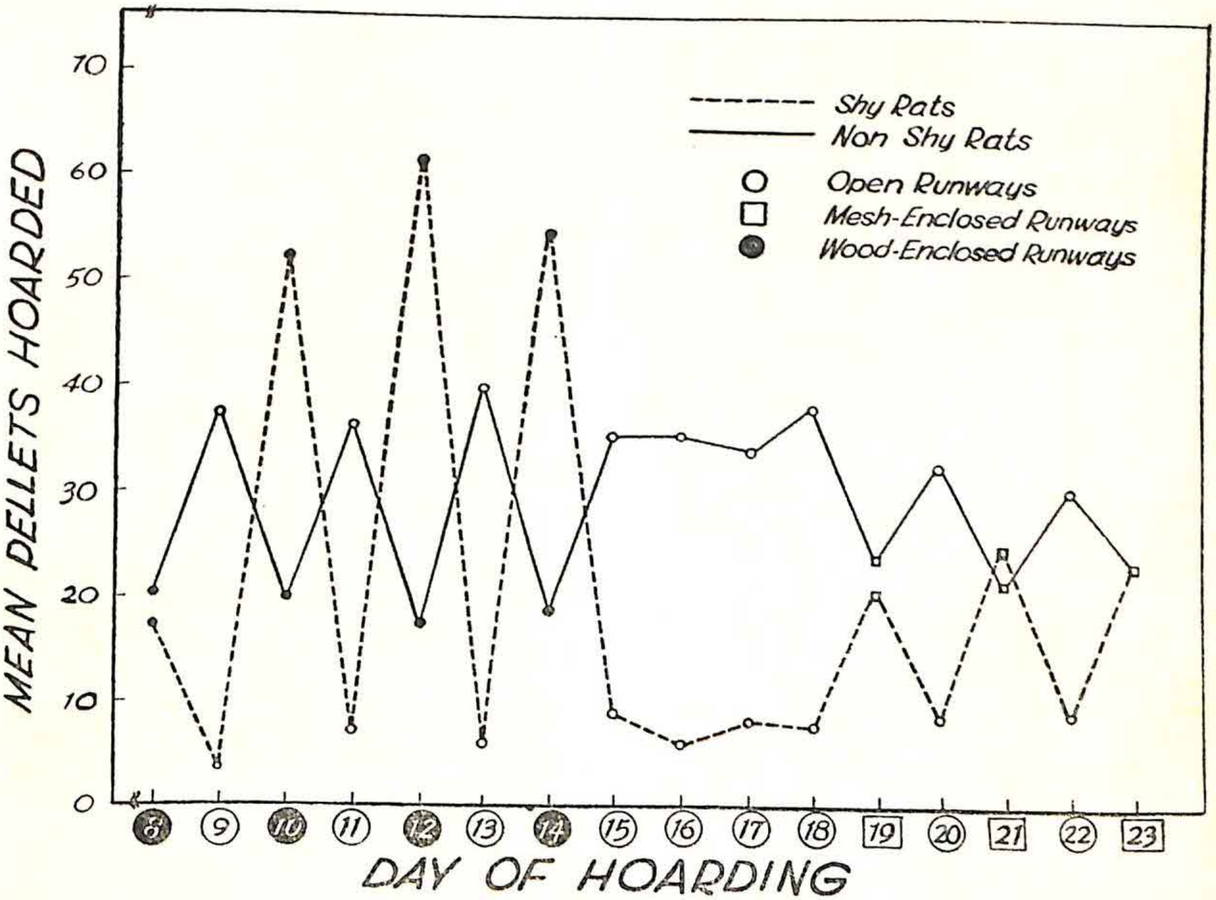

FIG. 3. Hoarding scores with "open" alley and two modifications of alley

The tests were the typical ones used in hoarding experiments and consisted of allowing *S*s to hoard for ½ hr. each day. Three pellets were fed after the ½-hr. test.

In part 1 of the tests only the unmodified open runway was used. In the second part the runway was modified as follows. On hoarding days 8, 10, 12, and 14, the closed runways were placed in the situation, and on days 19, 21, and 23 the mesh covers were used.

RESULTS

The mean hoarding scores of the *S*s used in the first part of the experiment can be seen in Figure 2. It will be seen that those *S*s which had been earlier classified as nonshy hoarded more pellets in the open hoarding situation than those which had been classified as shy. This same effect can be again seen in the scores represented in Figure 3. The mean hoarding scores on days when the open maze situation was used with this group of *S*s again show this same difference between groups classified as shy or nonshy.

The changes brought about by modifying the runways in the two previously described manners are indicated, beginning at the eighth day. It will be seen that as a result of enclosing the maze, the shy *S*s now hoard more pellets than do the nonshy *S*s. Finally, it will be noted that the scores obtained on days 19, 21, and 23, when the mesh covering was used, do not differ markedly for the two groups. It should be mentioned that the raw scores for 7 of the 12 individual *S*s are in complete agreement with the mean trend, while each of the remaining 5 *S*s has but a single score which is not consistent with the general trend.[1]

While the results obtained in the first part of the experiment, in which shy *S*s hoarded less than those classed as nonshy, appear at first to negate the finding of Bindra, it is soon apparent that what is happening here is that the shy *S*s do not venture onto the runway. This obviously makes hoarding impossible. At the same time the introduction of a closed alley has the effect of slightly decreasing the hoarding score for the nonshy *S*s, and the additional effect of a subsequent increase of hoarding when there is a return to the open situation. The scores of the shy *S*s show the opposite trend. Introduction of the closed alley causes a large increase in the mean number of pellets hoarded, and there is apparently some carry-over of this effect when the open situation is again used. Introduction of an open mesh covering, which should presumably cause a result lying somewhere between those obtained when using the open and closed alleys, indeed causes this result.

The results, then, seem to indicate that hoarding is influenced not only by physical make-up of environmental situations but depends to an equally important degree on the individual "personality" of the *S*. These results conform particularly well with those obtained by Bindra if we assume that on the basis of his selection procedure he chose *S*s which were predominantly nonshy.

CONCLUSION AND SUMMARY

The experiment reported in this paper confirms the security hypothesis offered by Miller and Viek and by Bindra. It demonstrates, in addition, that individual differences of shyness in rats effectively modify the behavior of these *S*s when hoarding under conditions differing in the amount of security they offer.

The general conclusions reached are that: (*a*) Nonshy rats hoard more pellets under open conditions which represent minimum security. (*b*) Shy rats hoard more pellets under conditions which offer moderate security between cage and hoarding bin.

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[1] Tables 1 and 2 showing hoarding scores of shy and non-shy rats may be obtained by ordering Document 3911 from the American Documentation Institute, Auxiliary Publications, Photoduplication Service, ℅ Library of Congress, Washington 25, D. C., remitting $1.25 for microfilm (images 1 in. high on standard 35 mm. motion picture film) or $1.25 for photocopies (6 in. by 8 in.) readable without optical aid.

THE EFFECT OF VARYING THE INTENSITY AND THE DURATION OF PRE-EXPOSURE UPON SUBSEQUENT DARK ADAPTATION IN THE HUMAN EYE[1]

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Several experiments have been carried out in order to determine the effect of varying the intensity and the duration of pre-exposure upon human dark adaptation. The interrelationships of intensity and time of exposure and their mutual influence upon subsequent dark adaptation are, however, still not clear, particularly for different values of time and intensity which fulfill the reciprocity relationship $I \times t = C$. In 1937 Wald and Clark (15) conducted an experiment in order to gather information bearing upon a specific hypothesis regarding the interrelationships of intensity and time of pre-exposure. Evidence had been presented (14) that the complete cycle of rhodopsin breakdown and regeneration involved, first, its conversion into retinene, thence to vitamin A, and back to rhodopsin. The regeneration could occur directly from the retinene stage or, more indirectly, from the vitamin A stage. In terms of the assumption that rod dark-adaptation is the expression of the increase in concentration of rhodopsin following its decomposition by light, Wald and Clark proposed that the two modes of rhodopsin regeneration should be reflected in measurements of dark adaptation. They predicted that following a short, intense pre-exposure, dark adaptation would be rapid; this would represent the predominance of the rhodopsin-retinene-rhodopsin mode of breakdown and synthesis. On the other hand, following a long pre-exposure, dark adaptation would be slow, representing the more circuitous mode of regeneration involving vitamin A. The predicted results were obtained; this means that pre-exposure time and intensity are not interchangeable variables with respect to their influence upon subsequent dark adaptation. Later, Haig (5) presented data showing that time and intensity are interchangeable, for a curve of rod dark-adaptation obtained after brief exposure to a high intensity was the same as one obtained after long exposure to a low intensity.

In the experiment reported here, we measured the course of human dark adaptation after pre-exposures covering a range of 1000 to 1 in both intensity and duration. The values of intensity and time were chosen so as to permit the investigation of the influence of the $I \times t = C$ condition of pre-exposure upon subsequent dark adaptation.

METHOD

Subjects and Apparatus

The authors served as subjects and experimenters. The apparatus used both for pre-exposures and threshold measurements was a monocular Hecht-Shlaer adaptometer mounted with the eyepiece projecting into a light-tight cubicle within the laboratory so that the subject could be dark-adapted regardless of the laboratory room lighting. The pre-exposure light was white, and its intensity was controlled by Wratten neutral tint, fixed filters. When threshold tests were made, a violet filter was used in conjunction with the instrument's black glass filters so that the subject could report on the presence of color at threshold. The threshold testing stimuli were presented by a pendulum-type shutter attached to the adaptometer, and their duration was 0.2 sec. All pre-exposures and test measurements were made through a 2-mm. artificial pupil inserted into the eyepiece of the instrument. The threshold test patch was 3° visual angle. The right eye was used, and both the pre-exposure and test stimuli were imaged 7° from the fovea on the nasal portion of the retina.

Procedure

The four intensities—6640, 664, 66.4, and 6.64 millilamberts (mL.)—and four durations—500, 50, 5, and 0.5 sec.—were investigated in all 16 combinations.

Each experimental session was conducted as follows: The subject entered the cubicle and was given a standard preliminary light-adaptation–dark-adaptation procedure. The stimulus was always 1610 mL. intensity, lasted for 1 min., subtended 35° visual angle, and was presented in the same position on the retina as the experimental stimuli. Threshold measurements were taken for 30 min., by which time the threshold values had reached a stable level. The experimental procedure was then begun. The intensity for that session was fixed by inserting the proper Wratten filters into the instrument, and the duration of pre-exposure was set on a stop clock. At a ready signal the subject looked into the instrument with his right eye, the light was turned on, and simultaneously the clock started. At the expiration of the pre-exposure time the adaptometer was shifted to the threshold testing position, and the initial threshold determined as quickly as possible, usually within 7 to 12 sec. This procedure was followed for all sessions except those requiring 0 5-sec. pre-exposure. For these sessions a variable electronic timer was used. The 0.5-sec. duration was set on the timer, an appropriate switch was thrown, and the light flashed on for a half-second and went off. The adaptometer was then quickly shifted to the threshold testing position, the light turned on again through its regular circuit, and test measurements were begun.

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[1] This research was carried out in the psychology laboratory of the University of Wisconsin. It was supported by the Research Committee of the Graduate School of the University of Wisconsin from funds appropriated for research by the State Legislature.

To obtain a threshold measurement the subject was first presented an intensity slightly higher than his previous threshold, a faintly visible stimulus. The intensity was then reduced to well below threshold, and the threshold value approached by intensity steps of 0.01 to 0.05 logarithmic units until the stimulus was reported as visible for two successive presentations. Threshold measurements were taken every half-minute for the first 5 min. and every minute thereafter.

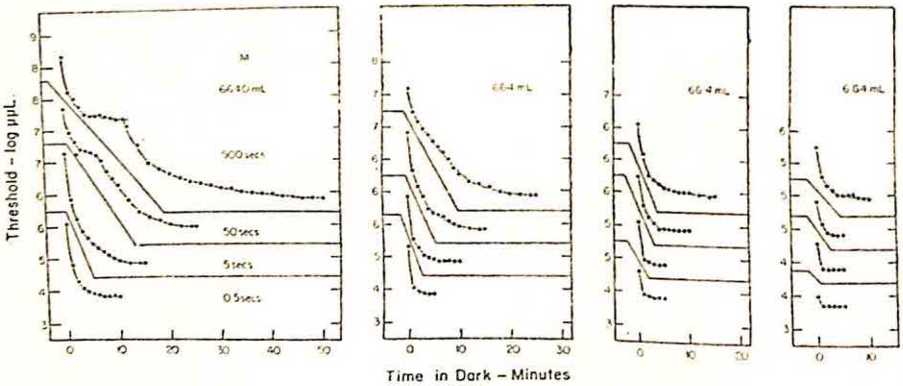

FIG. 1. The course of dark adaptation for subject F. A. M. for all intensities and durations of pre-exposure. At the top in each panel of the figure is given the value of the pre-exposure intensity. In the left-hand panel are given the durations of pre-exposure appropriate to each of the four curves; for the other three panels the order of the durations is the same as for the left-hand panel.

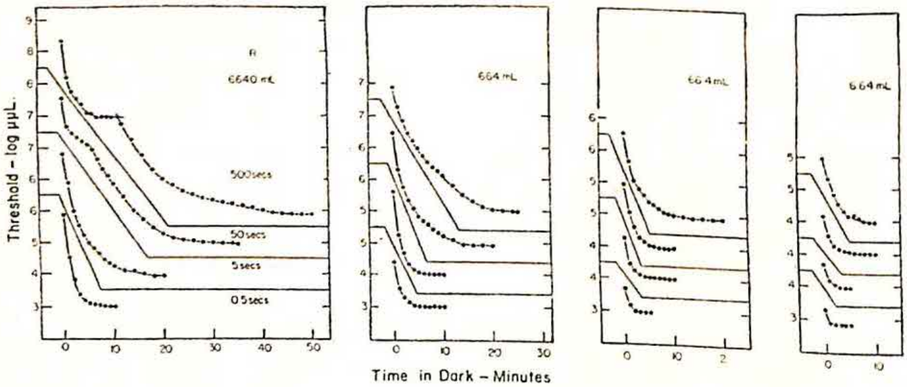

FIG. 2. The course of dark adaptation for subject A. J. R. for all intensities and durations of pre-exposure. The values of the intensities and durations in this figure are arranged as in Figure 1.

RESULTS

In all, 96 dark-adaptation curves were obtained—3 for each subject on each of the 16 conditions. Figures 1 and 2 show the averaged threshold values for each subject for all intensities and durations. The individual raw threshold values were recorded in log micromicrolamberts, and the points plotted on the graphs are the arithmetic means of these three sets of logarithmic values.

It can be seen that as either the intensity is increased or the duration extended, the initial threshold rises. For both subjects the effect of increasing the duration is more pronounced for the highest intensity than for the other three intensities. It is also clear that varying intensity at constant duration is more effective in raising the initial threshold value than varying duration at constant intensity.

Two other aspects of the data are the time of appearance of the discontinuity between the cone and rod portions of the curves, and the slope of the rod portion. For each subject there are two curves which show distinct cusps dividing them into two segments, the ones obtained after pre-exposure to 6640 mL. for 500- and 50-sec. duration. These curves show the relationship usually found between the degree of pre-exposure and the time of appearance of the cusp, i.e., the greater the degree, the later the cusp appears. Figures 1 and 2 reveal another aspect of the curves: As intensity decreases at constant duration of pre-exposure, or as duration decreases at constant intensity, the rod portions of the curves descend more rapidly to the final dark-adapted threshold value.

TABLE 1

Values of Pre-exposures in Millilambert-Seconds for All Combinations of Intensities and Durations for Which $I \times t = C$

PRE-EXPOSURE DURATION SECONDS	PRE-EXPOSURE INTENSITY			
	6640 mL	664 mL	66.4 mL.	6.64 mL.
500		332,000	33,200	3,320
50	332,000	33,200	3,320	332
5	33,200	3,320	332	33.2
0.5	3,320	332	33.2	

One of the main reasons for conducting this experiment was to obtain data upon the course of dark adaptation following pre-exposures in which the product of intensity *times* duration of exposure was constant. For 14 of the 16 combinations of intensities and durations the reciprocity relationship could be investigated. Table 1 presents these combinations in units of millilambert-seconds. Figures 3 to 5 show all the dark-adaptation curves for which the pre-exposure conditions fulfill the $I \times t = C$ condition.

The results obtained for these conditions of pre-exposure can be summarized as follows: (*a*) If the shape of the curve is taken as the criterion for comparison, it is seen that for 33.2 and 332 mL.-sec. (Fig. 3), there are no differences between any pairs of curves. For the range 6.64 to 664 mL. and 0.5 to 50 sec., intensity and duration are interchangeable variables. (*b*) For the six combinations of the product 3,320 mL.-sec. (Fig. 3), a similar situation holds. The only consistent difference to be found among the pairs of curves is the tendency for the one of each pair for the higher intensity and shorter duration of pre-exposure to have the higher initial threshold value. (*c*) Marked differences are found for two of the three comparisons for 33,200 mL.-sec. (Fig. 4). For both subjects the pair 6640 mL., 5 sec. versus 664 mL., 50 sec. are nearly coincident. For the other two pairs of curves the lack of coincidence is pronounced: in these cases the curve obtained after the higher intensity and shorter duration lies above the one for the lower intensity and longer duration. This means that for these pre-exposure times and intensities, the higher intensity and shorter duration results in a greater degree of light adaptation than the lower intensity and longer duration. (*d*) The curves of the pair for 332,000 mL.-sec. (Fig. 5) are also dissimilar. One curve for each pair has both rod and cone components, the other only the rod component.

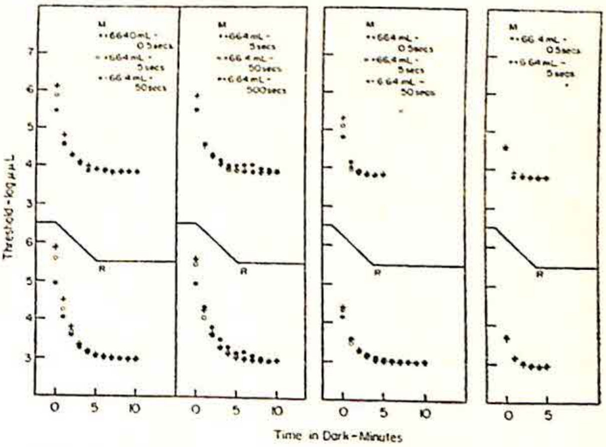

FIG. 3. The course of dark adaptation for both subjects following pre-exposure intensities and durations for which the product of intensity times time of pre-exposure is a constant. The value of the constant for the two panels on the left is 3320 mL.-sec.; for the middle panel, it is 332. mL.-sec., and for the right-hand panel, it is 33.2 mL.-sec.

DISCUSSION

There are two features of the data we wish to discuss. One is the variation in the values of the threshold at which the testing stimulus is last seen as colored, and the other is the interrelationships of intensity and time of pre-exposure for the reciprocity condition.

In Table 2 are given the threshold values which the subjects last report as being colored. A part of the evidence for the duality of the process of dark adaptation is the consistent result that, at moderate and high intensities of pre-exposure, the complete curve of dark adaptation is composed of two segments, a cone component and a rod component. When colored stimuli are used for determining the threshold, as in this experiment, it is usually found that the last colored stimulus occurs at the end of the cone component; this point is generally considered to mark the time of change from cone to rod adaptation. Table 2 shows that, at constant duration, there is a tendency for the lower intensities of pre-exposure to have lower threshold values at which color is still seen than is the case for the higher intensities, the difference attaining the order of 2 logarithmic units. The unusual feature of Table 2 is this marked variation in the values of the threshold at which color is last detectable in the test stimulus.

TABLE 2

Values of the Threshold in Log Micromicrolamberts at Which Color Was Last Seen in the Test Stimulus

PRE-EXPOSURE DURATION SECONDS	PRE-EXPOSURE INTENSITY			
	6640 mL.	664 mL.	66.4 mL.	6.64 mL.
	Subject F. A. M.			
500	5.99	6.00	5.55	5.41*
50	5.78	5.82	5.46	4.81
5	5.86	5.85	5.09	No color†
0.5	6.17*	5.22	No color	No color
	Subject A. J. R.			
500	5.83	6.22	5.52	4.73
50	5.85	5.98	5.10*	4.13
5	6.01	5.66*	4.17	3.69
0.5	5.87	4.38	3.85*	No color

* For one of the three experimental sessions at that intensity and duration of pre-exposure, color was not seen in any of the threshold testing stimuli.

† The entries labeled "No color" mean that for these intensitie and durations, color was not seen in any threshold test stimulus.s

Table 2 also shows that color is clearly seen in the early threshold stimuli of dark-adaptation curves which do not have distinct cone and rod components; consequently, it is difficult to know whether the thresholds of both types of receptor elements are indicated in such curves or only the thresholds of the rods. It has been stated (13) that the presence or absence of color is not a wholly reliable criterion of rod or cone function. If this is the case, it becomes a problem to determine what, indeed, are the cone and rod components of some of our curves. We have obtained many curves which show no cone component but for which the threshold stimuli early in the course of dark adaptation were clearly colored. In Figures 1 and 2 it is seen that for both subjects the curves for 6640 mL., 500 sec. pre-exposure have a distinct cusp separating them into the cone and rod components; the curves for 664 mL., 500 sec. do not. If the shape of the curves is taken as the criterion by which to judge whether both cone and rod thresholds have been measured, the 664 mL., 500 sec. curves indicate rod functioning only; there is no cone component. Yet, for both subjects—and at every session—for this intensity and duration of pre-exposure the early threshold stimuli were clearly colored, and the color was present for as long as four minutes before colorless stimuli appeared. A comparison of these two curves also reveals that the value of the initial threshold following the 664 mL., 500 sec. pre-exposure is much higher than the value of the first threshold after the cusp in the curve for 6640 mL., 500 sec.

We do not know why it is that colored threshold-testing stimuli are found over the more than 100 to 1 range (Table 2) nor why color is associated with the early thresholds for curves which show no distinct cone component. Hecht, Haig, and Chase (8), who report similar findings, mention the possibility that the color of the test stimulus may be important in determining the effect. It is also possible that in the intensity region of transition from cone to rod functioning, the value of the threshold is determined by neither type of receptor element alone but, instead, by both types interacting in some manner. Data on flicker fusion reported by Brooke (1) lend support to an explanation couched in such terms.

With respect to the reciprocity relationship of intensity and time of pre-exposure, a consideration of the results the authors obtained in a previous experiment upon the course of foveal dark adaptation (12) and the results reported by Crawford (2) and by Hartline and McDonald (7) led us to expect that probably we would find a similarity among the curves of dark adaptation following some pre-exposure conditions for which $I \times t = C$, and that among others we would not. The results of the present experiment show that, for the greater part of the conditions used, changing the pre-exposure intensity by a given factor has much the same effect upon subsequent dark adaptation as changing the duration by the same factor. The reciprocity relationship holds over a range of intensity and time of the order of 1000 to 1.

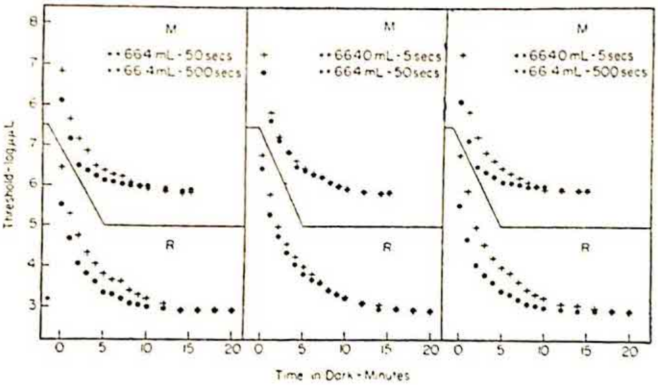

FIG. 4. The course of dark adaptation for both subjects following pre-exposure intensities and times whose product is 33,200 mL.-sec.

It is clear, however, that the reciprocity law does not hold for all the combinations of intensities and durations used in the experiment. This is most apparent in Figure 5, which shows the comparison between the curve obtained after pre-exposure to 6640 mL. for 50 sec. with that after 664 mL. for 500 sec. In this instance there is a prominent cone component on the higher intensity curve but none on the lower intensity one. This means, of course, that these conditions of pre-exposure have markedly different effects upon subsequent dark adaptation, for one of the results of the higher intensity is to raise the degree of light adaptation to the point that cone thresholds are obtained, an effect apparently not present at all after exposure to the low intensity. The failure of the reciprocity law is also found, however, in pairs of curves neither of which has a cone component (Fig. 4). The dissimilarities are clearly seen in the comparison of the 664 mL., 50 sec. versus 66.4 mL., 500 sec. and the 6640 mL., 5 sec. versus 66.4 mL., 500 sec.

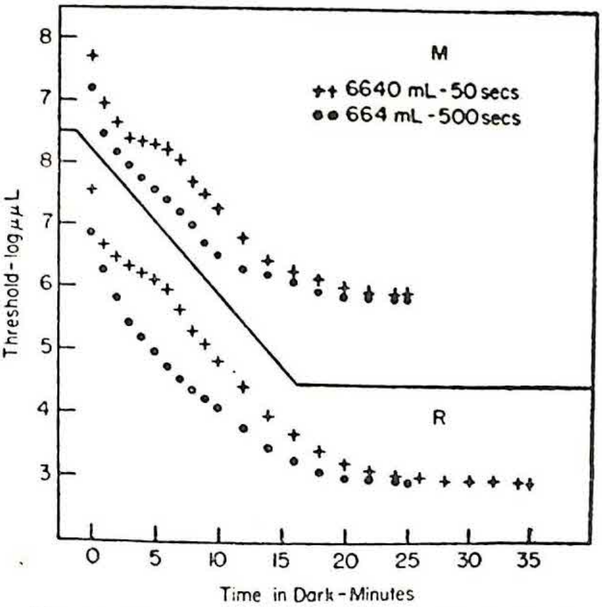

FIG. 5. The course of dark adaptation for both subjects following pre-exposure intensities and times whose product is 332,000 mL.-sec.

It has been suggested (5) that the finding that pre-exposure intensity and duration are interchangeable variables as they affect subsequent dark adaptation is an expression of the Bunsen-Roscoe law. Hartline (6) has shown that in the single optic nerve fiber response of *Limulus*, events occurring in the photoreceptor cell set an upper limit to the duration of the stimulus, at a given intensity, beyond which a further increase in duration is ineffective in modifying such features of the response as the latent period and the initial frequency of impulses. This "critical duration" is the maximum duration for which the Bunsen-Roscoe law of $I \times t = C$ holds at a given intensity; beyond this limit the relationship changes to $I = C$. The idea of the critical duration has been used by several experimenters (3, 4, 9, 10, 11) in interpreting data on human visual functions. In a human dark-adaptation study designed to test some theoretical considerations regarding retinal photochemistry, Crawford (2) used durations of the order of magnitude of the critical duration and found that for equal pre-exposure intensity *times* duration conditions at these short durations, the curves of subsequent dark adaptation were very similar. So far as we know, this is the only experiment upon human dark adaptation in which pre-exposure durations of the order of the critical duration have been used. If the similarity of the shapes of the curves is taken as the criterion, the data of Haig (5) and the results of the present experiment show that for durations longer than the critical duration, there exists some sort of reciprocal relationship between intensity and time of pre-exposure for a considerable range of these variables. There are, however, too few data upon the course of human dark adaptation showing the relationship between pre-exposure intensity and time for durations below the critical duration. We feel that until such data are available the problem of the Bunsen-Roscoe law as it relates to pre-exposure conditions in experiments upon human dark adaptation will not have been adequately explored.

SUMMARY

The recovery of dark adaptation was measured following all the combinations of intensities and durations of pre-exposure for four intensities (6640, 664, 66.4, and 6.64 mL.) and four durations (500, 50, 5, and 0.5 sec.). The measuring instrument was a Hecht-Shlaer adaptometer, and threshold tests were made for a parafoveal region, 3° visual angle in extent, centered 7° from the fovea on the nasal portion of the right retina. The pre-exposure stimulus was white; the threshold-testing stimulus was violet. All pre-exposure and test measurements were made through a 2-mm. artificial pupil. The authors served as experimenters and subjects, and each went through all 16 combinations of intensities and durations three times. The raw data were recorded in log micromicrolamberts. The values used in the analysis of the results were the arithmetic means of the three sets of logarithmic threshold values.

The chief results were as follows:

1. As pre-exposure intensity is increased (at constant duration) or duration is extended (at constant intensity), the initial threshold rises and the recovery of dark adaptation is retarded. When the pre-exposure intensity is increased by a given factor, the initial threshold value is raised more than if the duration is increased by the same factor.
2. There is a marked variation in the values of the threshold at which color is last seen in the test stimulus; following lower intensities of pre-exposure, colored stimuli are seen at lower threshold values than at higher intensities.
3. When the reciprocity relationship of pre-exposure for the different values of intensity and time for which $I \times t = C$ is investigated, it is found that there is little or no difference in the course of dark adaptation following degrees of pre-exposure equal to 3,320 ml.-sec. and below. For higher degrees of pre-exposure, 33,200 and 332,000 mL.-sec., marked differences are found; the higher the degree, the greater the difference.

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EFFECTS OF CORTICAL LESIONS ON MAZE RETENTION BY THE RAT[1]

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The experiments reported below began as part of an attempt to study the effects of neocortical lesions made after incomplete maze learning, upon subsequent acquisition. This plan aimed at determining whether Lashley's concept of "mass action" (3) held throughout the course of maze learning or whether different neocortical areas dominated the learning process at different times. A preliminary control group, operated after complete training in a multiple-T maze, showed no retention losses. Further experiments were conducted to explore the effects of larger lesions and of different maze types upon postoperative retention.

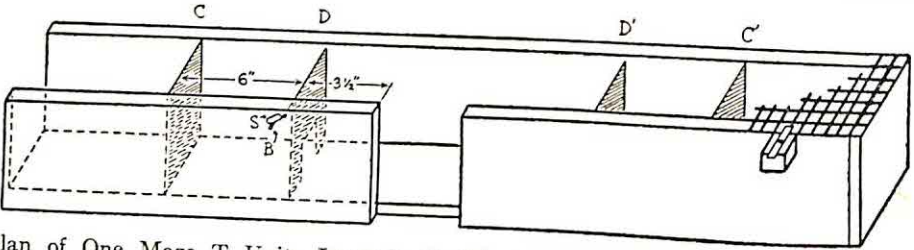

FIG. 1. Plan of One Maze T Unit. Legend: *C*, *C'*—curtains; *D*, *D'*—doors; *S*, mercury switch; *B*, wood-screw.

APPARATUS AND PROCEDURE

Two mazes, designated Maze T and Maze L, respectively, were used. Maze T was a 15-unit multiple-T maze where retracing was prevented. It consisted of interchangeable units such as shown in Figure 1. Each unit was made of ½-in. pine, painted flat black. Inside dimensions were 33½ by 2½ by 4 in. A black aluminum door hung in each arm 3½ in. beyond the center opening. A 1¼-in. square cut from the bottom of each door accommodated the *S*'s head. The door fastened to the long portion of an L-shaped shaft running through holes near the tops of the opposite walls of the unit. The short portion of the shaft hung outside the maze, forming a 60° angle with the door. When the door was raised 40°, a mercury switch attached to the short portion of the shaft closed and fired a tab in a 16-place elevator annunciator, which recorded errors. Each error-arm switch fired a separate tab; all switches for correct arm doors fired a single dummy tab. A wood screw just behind the short arm of the shaft for each correct side door blocked backward movement of the door, preventing retracing. A black curtain hung 6 in. beyond each door. Starting and goal boxes were 12 in. square and 4 in. deep; a 15-in.-long runway with a retracing door connected the starting box to the first unit. The entire maze was covered in units with ½-in. hardware cloth lids, held down by door buttons attached to wood blocks mounted outside the maze. The sequence of correct turns for Maze T was RLLRRL-RRLRLRLLR.

Maze L, a hand-scoring replica of Lashley's Maze III (3, pp. 30–31) was made from ½-in. pine painted flat black. Maze L was 4 in. deep and covered with a ½-in. hardware cloth lid. Both Maze T and Maze L were placed on the floor of a 14- by 24-ft. room illuminated by a single ceiling fixture with a 100-w. bulb.

Thirty-eight 120-day-old male Wistar albino rats were *S*s. Twenty-nine *S*s were trained in Maze T (Group T). They first learned to run from the starting box through the 15-in. initial runway to the goal box. The runway door was open at first and gradually lowered on subsequent trials. After *S*s finished preliminary training, the starting and goal boxes and runway were replaced in the maze. The *S*s then received one trial a day in Maze T until reaching a criterion of two successive errorless trials. The *S*s run in the preliminary experiment were operated after training, rested ten days, and retrained to criterion. The *S*s run in the main experiments were rested ten days after preoperative training, retrained to criterion, operated, rested ten more days, and finally retrained postoperatively. Nine *S*s run in Maze L (Group L) were treated by Lashley's procedure (3, p. 30). Both Group T and Group L worked under 22-hr. food deprivation and were regularly reinforced at the goal box with a pellet of mash. For each *S*, preoperative and postoperative trial and error scores were determined. Trial scores did not include criterion trials. Preoperative retraining scores were computed for *S*s run in the main Maze T experiments.

Operations were performed with ether anesthesia. After a midline incision, overlying muscle and periosteum were incised and reflected; the calvarium was thinned down with a boring drill and an opening made and enlarged with bone forceps. The dura was incised and reflected, and cortex was removed by pipette aspiration under double magnification afforded by a monocular eyepiece. The lesion area was covered with Gelfoam, and muscle and skin wounds were closed in anatomical layers. All operations were one-stage bilateral. After finishing postoperative training, the *S*s were sacrificed. Their brains were removed, fixed in formalin, embedded in tissue mat, cut at 30 micra, stained with thionin, and mounted. Lashley's method of reconstruction of lesions was used, and thalamic degeneration was determined using Lashley's thalamocortical map.

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[1] The author is greatly indebted to Dr. F. A. Beach for his generous aid during this experiment.

[2] NRC Fellow, 1950–1951.

RESULTS

Behavioral data for Groups T and L appear in Tables 1 and 2, respectively. In these two tables, *T* stands for trials and *E* for errors. Lesion reconstructions appear in Plates I and I.4.[3]

According to postoperative results, *S*s run in both the preliminary and main Maze T experiments could be classified into three subgroups: Group T-CorR, which had neocortical lesions and ran the maze after operation; Group T-CorF, which had neocortical lesions but refused to run the maze postoperatively; and Group T-RhinR, which had pyriform and mesocortical as well as neocortical damage and which ran the maze postoperatively. Of the 8 *S*s in the preliminary experiment, 7 fell into Group T-CorR and 1 into Group T-RhinR. The Fisher-Pitman randomization test (6) showed no significant differences at the .05 level between the 7 preliminary and 10 main-experiment *S*s in Group T-CorR as regards lesion size, preoperative training scores, or postoperative training scores, despite the fact that the main-experiment *S*s had preoperative retraining and the preliminary-experiment *S*s did not. Thus, all 17 Group T-CorR *S*s have been lumped together in Table 1. Nor were there any significant differences between the data from the 4 main-experiment *S*s and the 1 preliminary-experiment *S* classed in Group T-RhinR, and all these 5 *S*s have been lumped into one subgroup in Table 1. The only *S*s falling into Group T-CorF were 7 run in the main experiment.

Table 1 therefore shows means and standard deviations for neocortical lesion size and for preoperative and postoperative training scores of subgroups T-CorR, T-CorF, and T-RhinR separately. (Standard deviations are given for descriptive purposes only.) Application of the Fisher-Pitman randomization test showed no significant difference between the preoperative trial or error scores of any of the three subgroups in Table 1. On the other hand, the postoperative trial and error scores of Group T-RhinR are significantly different beyond the .001 level from those of Group T-CorR. Finally, the randomization test showed that lesion size for Group T-CorR, which ran postoperatively, differed significantly at the .05 level from that for Group T-CorF, which refused to run postoperatively. The amount of neocortical damage in Group T-CorR, however, did not differ significantly from that in Group T-RhinR.

TABLE 1

Behavioral Data for Group T

SUBGROUP		PER CENT LESION	PREOP. TRAINING		POSTOP. TRAINING	
			T	*E*	*T*	*E*
T-CorR	*M*	15.1	11.7	34.5	1.8	4.4
N = 17	σ	7.2	5.8	19.2	2.4	7.2
T-CorF	*M*	27.5	13.3	45.0	—	—
N = 7	σ	5.8	12.3	34.7	—	—
T-RhinR	*M*	9.5	18.8	56.6	28.6	85.2
N = 5	σ	4.7	17.2	49.4	24.8	83.0

TABLE 2

Behavioral Data for Group L

GROUP		PER CENT LESION	PREOP. TRAINING		PREOP. RETRAINING		POSTOP. TRAINING	
			T	*E*	*T*	*E*	*T*	*E*
Group L	*M*	24.0	46.3	117.9	14.4	3.7	58.2	153.1
N = 9	σ	5.2	64.0	122.9	16.1	4.1	45.9	121.3
Lashley Group	*M*	24.0	38.3	44.3	1.7	1.6	89.4	451.0
N = 9	σ	5.1	24.8	17.7	2.2	2.8	62.8	387.4

Table 2 presents means and standard deviations for lesion size, preoperative training, preoperative retraining, and postoperative training scores for Group L. This table also shows the same data for 9 *S*s with lesions comparable to those of Group L drawn from Lashley's retention-study data (3, pp. 92–93). (The Lashley *S*s are numbers 92, 93, 94, 96, 103, 108, 109, 112, and 116.) One Group L *S* failed to relearn the maze postoperatively as against 4 Lashley *S*s. The randomization test showed a significant difference between the two groups on preoperative retraining trials only. Statistical comparisons between the two groups must be viewed cautiously, however, since the groups came from different strains and were run under different conditions.

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[3] Table 3, showing a detailed analysis of thalamic degeneration and subcortical damage, which was deposited with the American Documentation Institute, was unfortunately lost in the move of the Institute to the Library of Congress. We deeply regret this loss. (Editor's Note)

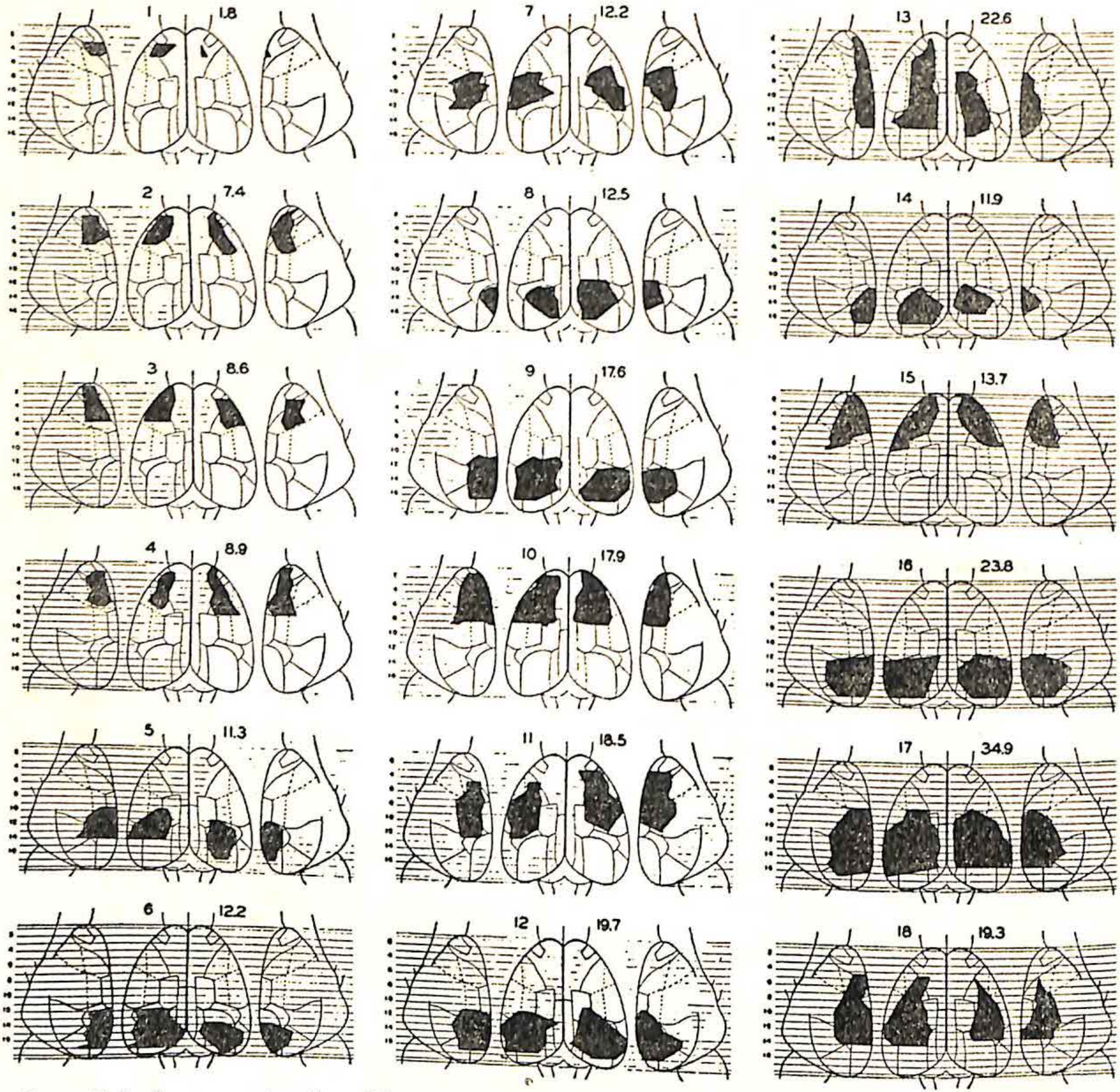

PLATE I. Surface reconstruction of lesions. Numbers 1 to 17, Group T-CorR; 18 to 24, Group T-CorF; 25–29, Group T-RhinR; 30 to 38, Group L. Serial numbers and per cent neocortex removed are at top and right, respectively, of each diagram.

DISCUSSION

Inspection of data from Group T-CorR, which ran after neocortical lesions, shows little postoperative deficit when lesions are below 15 per cent. Lashley's data on maze retention after cerebral damage show a similar tendency. Thus, "mass action," the correlation between lesion size and behavioral deficit, may not appear until a certain minimum lesion size, about 15 per cent, has been passed.

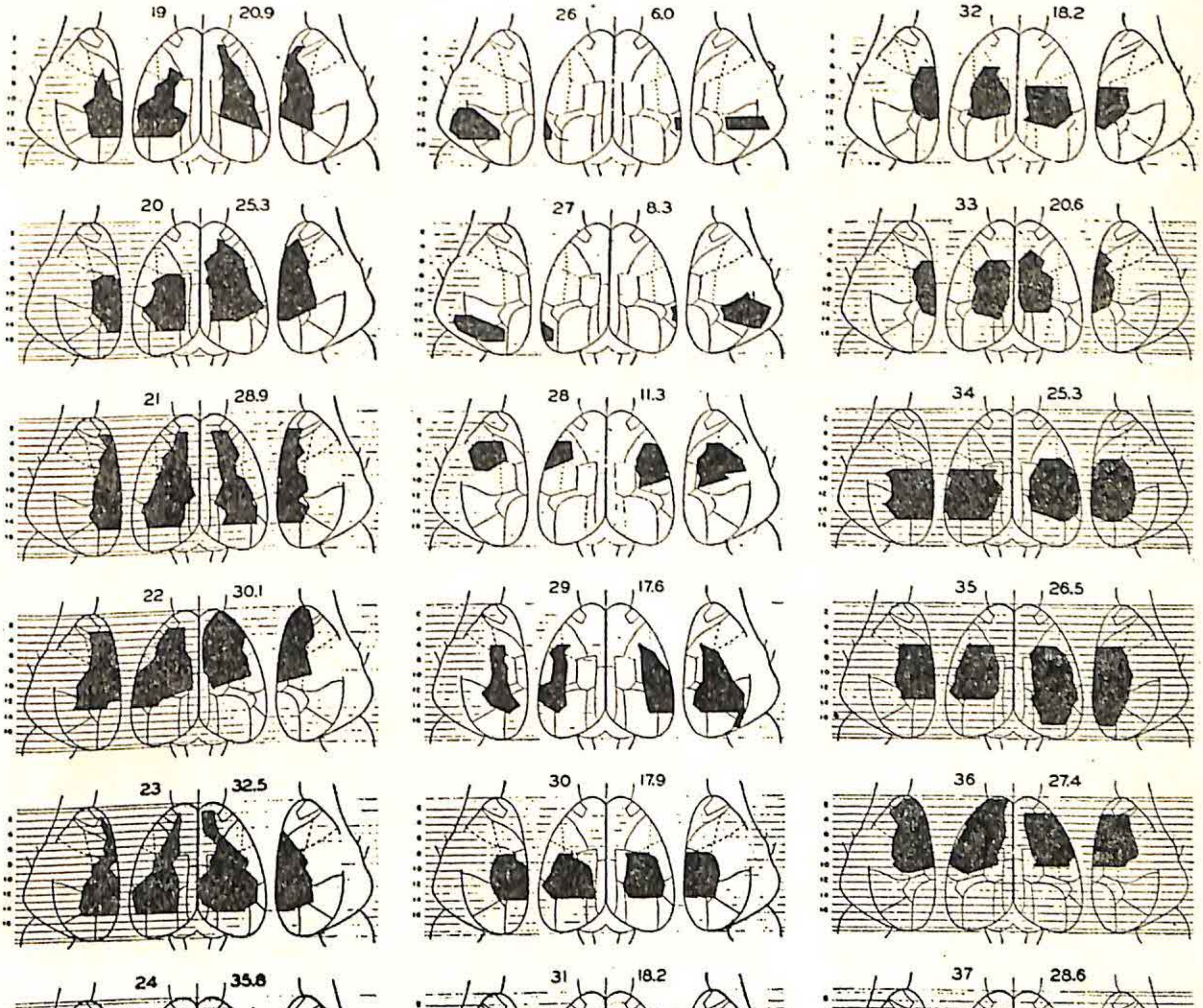

PLATE IA. Legend as in Plate I.

On the other hand, when lesion size exceeded 20 per cent in Group T, the *S*s tended to refuse to perform postoperatively (Group T-CorF). This refusal to run may be due to appearance of an "aversion" toward operating the swinging doors of the maze. Group L, in a retracing maze with no such doors, ran after lesions exceeding 20 per cent. Furthermore, Ericksen (2) reports that in a nonretracing maze with drop-doors operated by the experimenter, no *S* refused to run the maze after lesions exceeding 20 per cent. In latch-box tests, Lashley (4) reports that after operation, *S*s "lacked aggressiveness" in operating the necessary apparatus. The nature of such a refusal of the Group T *S*s to operate the maze doors is not at all clear at present; its appearance, however, would mask any signs of "mass action," since the *S*s do not perform and hence cannot make postoperative scores.

When lesions invaded mesocortex and allocortex, a different postoperative picture appeared. Removal of phylogenetically older cortex along with neocortex produced significantly poorer postoperative scores than removal of neocortex only, the same amount of neocortex being destroyed in both cases. Thus, mesocortex and allocortex play a role in maze retention. Whether this is the same role played by neocortex and whether the older cortex operates on a "mass action" basis remain to be determined. Using different *S*s and different tests, other experimenters have reported learning losses after temporal lobe lesions. The present finding that rhinencephalic lesions interfere with retention of a maze habit may bear some relation to the latter studies.

Finally, the data from Group L show lower mean postoperative scores than those from the group of "comparable" Lashley *S*s, which had cautery lesions of the same size. The differences in postoperative scores between the two groups are not statistically significant. In consideration of the small numbers of *S*s and the difficulties of interpreting any statistical tests, no conclusions should be drawn from these data. The data suggest, however, that it would be worth while to explore differential effects on behavior from cautery as against aspiration lesions, particularly in view of recent biochemical evidence (1) which shows effects of cautery extending far beyond the bounds of the lesion as determined by standard anatomical techniques.

SUMMARY AND CONCLUSIONS

Twenty-nine male albino rats (Group T) were trained in a nonretracing multiple-T maze and then subjected to aspiration lesions. Nine others were trained in a retracing maze (Lashley's Maze III) and then operated (Group L).

1. Neocortical lesions below 15 per cent produced little or no postoperative loss in Group T. This lack of effect of relatively small lesions may be a factor limiting "mass action."
2. Neocortical lesions over 20 per cent tended to make the *S*s in Group T refuse to run the maze. This refusal seems due to an aversion toward operating the swinging doors used in the maze.
3. Allocortex and mesocortex appear to play a role in maze retention.
4. The question is raised as to possible differences between the effects of cautery and aspiration lesions of the same apparent size on behavior.

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THE EFFECTS OF NEONATAL ANOXIA ON THE MAZE PERFORMANCE OF ADULT RATS

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The effects of paranatal anoxia upon the later adaptive behavior of mammals is a question of considerable theoretical and practical interest. Clinical (6, 7) and experimental attention is being increasingly directed toward the problem. Windle and Becker (10) operatively delivered guinea pigs at near term and subjected certain of the animals to severe anoxia by reducing the blood supply of the experimental animals *in utero*. The authors report a considerable reduction in the maze performance of the surviving animals when they are compared with litter mates similarly delivered but not exposed to experimental anoxia. More recently Meier and Bunch (5) report a reduction in learning, relearning, and habit reversal when newborn rats are subjected to 30-min. exposure at less than 3 per cent oxygen equivalence and then trained on a single-T water maze at 100 days of age. However, most of the differences between experimental and control rats were not statistically significant.

The present study tested the effects of neonatal anoxic exposure in mature rats by measuring their performance on a complicated maze. The two degrees of anoxia used were selected because of their relatedness to previous experiments. One condition of anoxia, 38-min. stay at a simulated altitude of 34,000 ft., was used because it is an amount of anoxia which results in a 50 per cent survival rate in adult male rats of the strain used in this experiment. As part of another unpublished study 120 male albino rats 100 days of age were subjected to an altitude equivalent of 34,000 ft., ascending at a rate of 1,500 ft. per minute and record was taken of the length of survival of individual animals. It was found that the median survival time at this pressure was 38 min. This time approximates that reported by investigators using other strains of rats (8). Also, the cumulative anoxia resulting from a 38-min. stay at 34,000 ft. approaches the amount of anoxia induced by Meier and Bunch when they exposed rats 30 min. at a 3 per cent oxygen level (34,000 ft. simulated altitude is equivalent to a 5 per cent environmental oxygen level). The other degree of anoxia used in the present study, 3 hr. at 30,000 ft., is an amount of anoxia known to reduce maze performance and cerebral cortical cell density in mature rats (3, 4).

PROCEDURE

Subjects

These were newborn albino rats of the Harlan strain. Five litters comprising a total of 44 rats were used in the experiment.

Induction of Anoxia

Within an average period of 1 hr. after the birth of the last rat in a litter, the litter was approximately divided among control and experimental groups. The experimental *S*s were marked and placed in a small container lined with wood shavings. The container was immediately placed in a decompression chamber and the chamber evacuated at a rate of 1,500 ft. per minute simulated altitude until the desired altitude was reached. One-half of the experimental *S*s stayed at a simulated altitude of 30,000 ft. for 3 hr.; the other half of the experimental *S*s stayed at a 34,000-ft. pressure equivalent for 38 min. The control litter mates were kept in a similar container away from the mother for an equal period of time. Following this procedure all rats of a litter were returned to the home cage and remained with the mother until they were weaned at 30 days of age. At weaning the rats were sex-segregated and maintained in the laboratory until they were 100 days old.

Maze Training

This was identical with that reported in an earlier study (3), and that report should be consulted for details. Beginning at 100 days of age the *S*s were handled 5 days on a table with food present, then on the sixth day started on straight-a-way training under 23-hr. drive and rewarded in the goal box with 45 sec. of ad lib. eating of Purina dog pellets. Immediately following the second trial the *S*s were permitted 1 hr. of ad lib. feeding and drinking. After 5 days, two trials per day, straight-a-way training, *S*s began training on a Stone multiple-T alley maze. Here, again, they were on 23-hr. hunger drive, reinforced in the goal box with 45 sec. of ad lib. eating, and received two daily trials followed by 1 hr. of eating until they reached a criterion of three out of four errorless trials.

RESULTS

Physiological

None of the *S*s exposed to these two conditions of anoxia died within the 190-day period of observation entailed by this experiment. These data contrast with the 50 per cent survival of adult rats (100 days of age) of this strain when exposed for 38 min. at a simulated altitude of 34,000 ft. and to the approximate 10 per cent loss which we have encountered in 100-day-old rats exposed for 3 hr. at the 30,000-ft. altitude equivalent. The greater survival of the newborn rats is not surprising since previous investigators have reported that newborn rats display greater resistance to anoxic exposure than do adult rats (1, 2).

TABLE 1

Relationship Between Neonatal Exposure to Anoxia and Maze Performance in Maturity

DEGREE OF ANOXIA	MEASURES OF MAZE PERFORMANCE					
	Errors		Time		Trials	
	Mean	*SD*	Mean	*SD*	Mean	*SD*
Zero	94.4	28.0	1,491.2	535.0	34.6	15.1
3 hr. 30,000	87.2	37.2	1,304.5	427.2	33.4	15.2
38 min. 34,000	105.1	16.1	1,619.0	998.0	37.6	22.1

No gross neuromuscular defects were observed in the experimental *S*s of the present study.

Psychological

The maze records of the control and experimental groups are summarized in Table 1. The 14 *S*s exposed 3 hr. at a simulated altitude of 30,000 ft. surpassed all other groups in maze performance; the 18 *S*s in the control groups were next in adequacy of maze performance; and the 10 *S*s exposed 38 min. at 34,000-ft. altitude equivalent did poorer than any of the groups studied; however, none of these differences reached the 5 per cent significance level.

DISCUSSION

The slight impairment in maze performance found in our 38-min., 34,000-ft. group may be interpreted as supporting the finding of Meier and Bunch that this approximate level of anoxia in the neonatal rat results in a small reduction in maze-learning efficiency at maturity. It must be recognized, however, that statistically significant differences were not found in either study.

The results observed in the group exposed 3 hr. at 30,000-ft. simulated altitude are interpreted as indicating that anoxia sufficient to impair considerably the maze performance of adult rats does not materially affect the maze behavior of rats undergoing such an exposure near birth. One of us has described a significant reduction in the maze performance of *adult* rats exposed to 0, .5, 3, and 6 hr. at 30,000-ft. simulated altitude and then trained on a 14-unit maze 6 days or 42 days after anoxic exposure (3). Since a sample of exposed *S*s drawn from this study was shown to have suffered significant cerebral cortical deterioration, it was concluded that the loss of brain tissue in the anoxia-exposed *S*s was the best explanation of their reduced maze performance (4). A possible explanation of this difference in the effect of anoxia on neonatal and mature rats is that the young rats do not suffer as much neural damage as adult rats. This can be inferred from the known age differences in survival of anoxic insult (1, 2). Another possible explanation of the age difference in the behavioral effects of anoxia is that even though the neonate suffers brain damage comparable to the adult rat, there is a differential behavioral effect of such damage as a function of the age of the brain-damaged animal. There is evidence that brain damage in infancy is less disruptive of maze performance than quantitatively and qualitatively similar brain damage in the mature rat (9).

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THE EFFECT OF ELECTROCONVULSIVE SHOCK ON A CONDITIONED EMOTIONAL RESPONSE: THE EFFECT OF ELECTROCONVULSIVE SHOCK UNDER ETHER ANESTHESIA[1]

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During the past few years, several investigators have reported that ECS does not have its usual effects on rats if the convulsions are prevented from occurring by anesthesia at the time of treatment. Heilbrunn (2) found that 7 of 11 rats given five ECS's under light ether anesthesia showed only a mild muscular contraction when the current passed. More important, none of these 7 animals showed histological signs of intracranial hemorrhage post-mortem. Each of the other four animals showed one or two severe muscular contractions in response to the current. Three of these showed histological signs of intracranial bleeding. The difference between the two groups in incidence of hemorrhage is significant ($\chi^2 = 3.93$, $.02 < p < .05$, computed by the present authors). Heilbrunn argued that the hemorrhage is produced by the increased vascular tension associated with the muscular contractions of a convulsion rather than by the passage of the electrical current itself.

This argument would suggest that ECS might not have its usual effects on behavior if the convulsions were blocked or attenuated by anesthesia at the time of treatment. Porter and Stone (5) checked this possibility with maze experiments in which one group of animals received ECS alone and one group received ECS while under ether anesthesia. They found that the ether-ECS animals did not show the decrements in maze performance found among the regular ECS animals during the treatment period. In a second experiment they did find, however, that the ether-ECS animals failed to show the usual improvement from trial to trial during the treatment in running a maze that they had not yet learned to criterion.

Following this line of thought, Stone and Walker (9) made a preliminary study of the effect of ECS under ether anesthesia on gestation and maternal behavior. Rosvold (6) had found that ECS, if given to rats at the proper points in time, tends both to interfere with normal gestation and to disrupt the patterns of maternal care of newborn infants. The Stone and Walker report suggests, however, that ether anesthesia at the time of treatment tends to block this effect of ECS.

Siegel, McGinnies, and Box (8) investigated the power of Nembutal anesthesia to prevent ECS from having its adverse effects upon runway performance. They were interested not only in confirming the earlier findings but also wanted to determine whether the anesthetic alone would have any adverse effect on performance, a possibility not investigated by Porter and Stone. Accordingly, Siegel and his coworkers employed three groups—one group of rats received a saline injection prior to ECS, one group received a Nembutal injection prior to ECS, and one group received Nembutal only. Each animal received one treatment as indicated after training in the runway. A test 8 hr. after treatment revealed that only the saline-ECS group showed impaired performance. The other two showed none. The authors concluded that the anesthesia protected the treated animals either by preventing the convulsion or by insuring the central nervous system in some way against the disturbance caused by passage of the electrical current used in ECS.

The present experiment was designed to check on the previous findings regarding the "protective" effect of ether anesthesia at the time of ECS treatment. In addition, it includes a control for the effects of interaction between ECS and anesthesia. The previous reports have argued that the anesthesia prevents ECS from having its usual effects by prevent-

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ing the convulsion. Perhaps, however, some consequence of ether other than its anticonvulsant effect is critical here. Though it seems unlikely, the "protective" effect of ether may be unrelated to its anticonvulsant properties; the protective effect might also appear if ether is given at a time when it would not prevent convulsions. For this reason, the present experiment includes a group of animals that received both ECS and ether but at different times so that the convulsions occurred in the usual way.

In addition, two of the previous experiments employed behavioral tests which emphasize locomotion or motor performance to some degree—the maze and the runway. In itself, this feature of the experiments is not too critical. Ataxia or incoordination, as a by-product of injury to the peripheral effector apparatus sustained during the physical stress of ECS convulsions, is as legitimate an effect of the treatment as any other. But in assessing the role of the convulsions, as such, in producing the effects of ECS, it would seem worth while to distinguish between motor impairments and psychological changes following the treatment. The two kinds of effects are not necessarily the same. An anesthetic which blocks the convulsion may prevent ECS from having its typical effect in test situations which depend upon locomotion to any significant degree. But it would not necessarily follow that the anesthetic would prevent ECS from having its typical effect on the retention of a simple conditioned discrimination. While the report by Stone and Walker certainly suggested that blocking the convulsion with ether does more than simply prevent torn ligaments and fractures, it still seemed worth while to check the previous results in a somewhat different experimental situation.

The present experiment employs a test situation in which the effect of ECS appears as in increase in activity. Previous research (1, 3, 4) has indicated that ECS can weaken a conditioned emotional response (CER) which consists of cessation of lever pressing in a Skinner box. If ECS has its usual effect, if the treatment weakens the CER, the animals no longer show this cessation in lever pressing. The effect of ECS thus appears as an increase in activity. Conversely, if something blocks ECS from having its usual effect, the net outcome is either no change or a decrease in activity in that the animals still show the plateau in the lever-pressing curve after treatment. Thus, animals made ataxic, poorly coordinated, or somatically ill by ECS would tend to produce curves on a post-ECS retention test similar to the records produced by untreated controls or animals upon which the treatment had had no effect.

METHOD

Subjects

Forty-six naive, male albino rats, 60 to 70 days old at the beginning of the experiment.

Conditioning Procedure

The conditioned emotional response (CER) was established in Skinner boxes in accordance with our standard procedure described elsewhere (4). In brief, all *S*s were first trained in lever pressing until they showed a fairly even, stable output of lever responses, first for a regular and then for an aperiodic water reward. Then, each *S* received five emotional conditioning trials, each consisting of a 3-min. presentation of a clicking noise (the conditioned stimulus) terminated contiguously with two momentary, painful electric shocks to the feet (approximately 1.5 ma.) as the unconditioned stimulus, delivered through the grill floor of the apparatus. Most of these conditioning trials were spaced several days apart, with adaptation runs intervening, and only one trial was given on any one day in order to minimize the development of generalized fear reactions to the apparatus. Records were kept of the lever-pressing output for the first, second, third, and fourth 3-min. segments of the daily 12-min. runs. For all conditioning and retention test trials, the clicker was introduced at the beginning of the fourth minute and the unconditioned shock stimuli, if given, were introduced at the end of the sixth minute, when the clicker was turned off. As indicated above, the CER in this situation consists of a marked reduction or complete cessation in lever pressing during presentation of the clicker.

Electroconvulsive Shock and Anesthesia

The experimental treatments began on the fourth day after the last emotional conditioning trial. The *S*s were divided into three groups, roughly equated in terms of the magnitude of the CER which appeared on the fifth conditioning trial.

Group I. The 15 *S*s of this group received 14 ECS's, 1 on the first treatment day, 2 per day for the next six days, spaced 4 to 6 hr. apart, and 1 on the last day. The apparatus and procedure for ECS were the same as those employed in previous experiments (3). The apparatus delivers 50 to 54 ma. for 0.18 sec. through moistened electrodes clipped to the ears. Three *S*s in this group died or were crippled as a result of the ECS; 12 completed the experiment.

Group II. The 15 *S*s of this group received 14 ECS's according to the same schedule as followed for Group I. Each *S* was anesthetized just before each treatment by being placed in a desiccating jar and allowed to inhale ether vapor until it had lost its corneal reflex. Then, the *S* was given ECS immediately. No *S* died as a result of this procedure; no *S* had a convulsion. Each *S* showed a mild, general tonic muscular contraction during passage of the current, a contraction like that which can be elicited for the first minute or so after an animal has died.

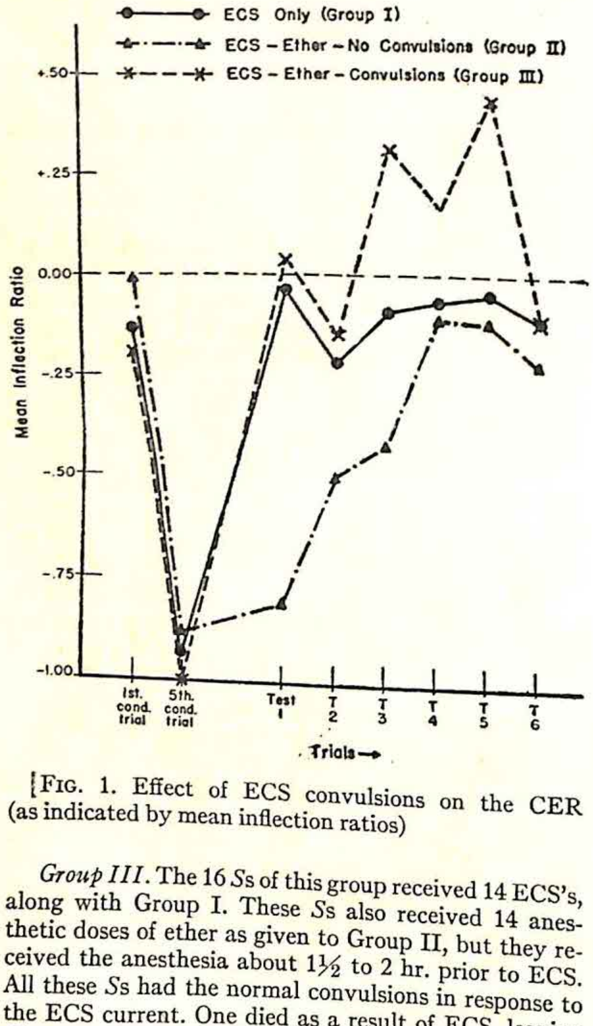

FIG. 1. Effect of ECS convulsions on the CER (as indicated by mean inflection ratios)

Group III. The 16 *S*s of this group received 14 ECS's, along with Group I. These *S*s also received 14 anesthetic doses of ether as given to Group II, but they received the anesthesia about 1½ to 2 hr. prior to ECS. All these *S*s had the normal convulsions in response to the ECS current. One died as a result of ECS, leaving 15 to complete the experiment.

Retention Tests

Beginning on the fourth day after the last treatment, and after two adaptation runs, all *S*s received a total of six retention tests, one per day for six successive days. Each test consisted of an unreinforced presentation of the clicker during the daily run in the Skinner box. This procedure allowed for two somewhat different measures of the strength of the CER which might survive each of the three types of treatment. The tests produced indications of the amplitude of the CER, expressed in terms of the decrease in lever-pressing output during the clicker, on each of six successive days. In addition, this arrangement also provided some measure of the strength of the CER in each group as indicated by resistance to experimental extinction. Each retention test, because it includes an unreinforced presentation of the conditioned stimulus, is, in a sense, an extinction trial.

All *S*s were on a 23-hr. water-deprivation schedule during conditioning and during the retention-test period but had free access to food and water in the home cages during the treatment period.

RESULTS AND DISCUSSION

In general, the results of this experiment confirm the earlier reports by other investigators. Twelve of the 15 *S*s in Group II, whose convulsions were blocked by ether anesthesia, showed the CER at full strength after treatment by a complete cessation of lever pressing during the clicker on test 1. In contrast, only one *S* out of each of the other two groups (I and III), which had the usual ECS convulsions, showed the full CER on test 1. These differences between Groups I and II and between III and II were both significant at <.01 level of confidence (χ^2 values of 10.99 and 13.57, respectively). And the difference between Groups I and III was not significant.

Figure 1 illustrates the results of the experiment in somewhat more graphic detail. The figure shows the average value of the "inflection ratio" for each of the groups for the first and fifth conditioning trials and the six retention tests. The "inflection ratio" indicates how much and in which direction the clicker, during the second 3 min. of the trial, changes the output of lever responses (see 4 for a more complete discussion of the ratio). It expresses the difference in output between the first and second 3-min. segments of the curve as a fraction (percentage in decimal form) of the output during the first 3-min. segment. (The inflection ratio $= \dfrac{B - A}{A}$, where A is the number of lever responses made during the first and B is the number made during the second 3-min. segment of the curve.) Complete cessation of lever pressing during the clicker (or second 3 min. of the curve) appears as a ratio of -1.00, essentially unchanged output appears as a ratio of around 0.00, and a 100 per cent increase in output appears as a ratio of $+1.00$.

The sharp drop toward -1.00 between the first and fifth conditioning trials for all groups reflects the development of the CER. The sharp rise in the curves for Groups I and III between the fifth conditioning trial and test 1 reflects the weakening effect of the ECS convulsions on the CER. In contrast, the curve for Group II, which had no ECS convulsions because of the ether anesthesia, indicates that the CER was still strong on test 1 and remained so for tests 2 and 3.

The difference between Groups I and III for tests 3 through 5 is more apparent than real. One *S* in Group III showed atypical and highly variable output curves for these trials. With this *S* excluded, the curves for Groups I and III do not differ materially, though the average ratios for Group III fairly consistently tend to be slightly above those for Group I, and variability from trial to trial among the Group III *S*s tends to be somewhat greater.

The results of this experiment clearly indicate that ECS does not have its usual marked effect upon the CER if ether anesthesia prevents the convulsions from occurring. And the similarity between Group I, which received ECS only, and Group III, which received both ECS and ether but at different times to allow the convulsions to occur, indicates that the convulsions themselves play an important role in weakening the CER. The *S*s in Group III show the typical weakening of the CER after treatment, even though they received as much anesthesia as Group II *S*s.

These results, moreover, agree with the outcome of previous experiments which used the maze and runway. All the experiments, taken together, indicate that the convulsions associated with ECS do something more than just injure the peripheral motor apparatus to produce post-ECS decrements in tasks involving locomotion simply by slowing *S* down or making it stiff and sore. In addition, these results are consistent with, but do not necessarily confirm, the notion that intracranial hemorrhages caused by the convulsions play an important role in producing the ECS effect (see 2). Histological data were not obtained from the *S*s in the present experiment. To allow a thorough check on the effect of convulsions on behavior, we kept the *S*s alive a little too long after treatment to provide the best histological data for this purpose. We plan to obtain such data in the near future, however.

The data from the present experiment do not necessarily indicate that passage of the ECS current alone, in those *S*s where ether blocked the convulsion, has no effect on the CER. Nor do the results necessarily indicate that ether, given at such a time as to allow normal convulsions to occur, does not interact with ECS in weakening the CER. The present experiment only indicates that the convulsions have a considerably greater influence on the CER than either of the other two factors. Both of these other factors are now under investigation, using a weaker CER to check on the effect of the ECS current alone and a stronger CER to check on the interaction between ether and ECS when convulsions are permitted to occur. This adjustment in strength of the CER is necessary if the main effect in each of the two comparisons is to have a reasonable chance of appearing clearly in the retention tests after treatment.

The present data are also quite consistent with the hypothesis that at least a portion of the effect of ECS may be attributable to a general physiological reaction to stress (7, 8). Anesthesia prevents what may be the most stressful aspect of ECS—the convulsions—and in doing so prevents ECS from having its usual substantial effect on the CER. The data by no means confirm the hypothesis, however. A decisive confirmation would require the demonstration that other stress-producing agents have the same effect upon the CER. Research on this possibility is now in progress.

CONCLUSIONS

1. The effect of ECS upon the conditioned emotional response is markedly attenuated in *S*s prevented from having the convulsions by ether anesthesia just before treatment. This attenuation does not appear if ether and ECS are given at different times so that the *S*s have the usual convulsions; it appears to be related definitely to the prevention of the convulsions by the anesthetic.

2. This experiment does not rule out definitely the possibility that the ECS current alone, when convulsions have been prevented by anesthesia, has some effect upon the conditioned emotional response. Nor does it

rule out the possibility that ECS and ether, given at different times, may interact to some degree in weakening the conditioned emotional response. The data do indicate, however, that the effect of either of these two factors upon the conditioned emotional response, if they have any effect at all, is probably small in comparison with the substantial effect of the convulsions.

3. The data from the present experiment confirm previous findings on the effect of blocking the convulsions in ECS with an anesthetic. The present results, given the test situation in this experiment, also indicate that ECS does not produce its effects on behavior solely by injuring the peripheral effector apparatus in such a way as would impair locomotion and motor coordination, an interpretation not clearly ruled out by the previous experiments which used the maze and runway.

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THE EFFICIENCY OF THE SERIAL MULTIPLE VISUAL DISCRIMINATION APPARATUS AND METHOD WITH WHITE RATS

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It is well known that the original training is the most tedious part of any animal performance study. Months may be spent in training animals for an experiment where the crucial data may be secured in a matter of seconds. In some of these studies the animals are either unfit for further work, or they must be kept for long periods to determine mortality data. In either case it becomes necessary to train a new group of animals. Where fine sensory thresholds are sought, the demands on personnel and time are greatly magnified. It has therefore become necessary to scrutinize existing apparatus and methods to see if the same level of training might not be achieved in a more economical manner.

The first efficient visual discrimination apparatus for rats was developed by Lashley (4). The essential point in his technique was that the rats were required to slow down in front of the stimulus patterns before they jumped across a gap to the positive figure. The extra attention secured in this manner plus the immediacy of reward or punishment was conducive to high accuracy of response.

Fields (1) used the essential "jump across a gap" but increased the number of stimulus openings to five. These and other changes described by him were responsible for an increase in efficiency in the original training period and a greater increase in statistical reliability when thresholds were sought.

The apparatus and techniques to be described here are simply logical combinations of the five-choice multiple-stimulus jumping apparatus used with rats (1) and the serial two-choice, five-box apparatus used with raccoons (2). The latter idea was taken from Stone's earlier serial apparatus (6, 7). Although the SMVDA idea was discussed with Dr. Stone in 1931, the unit in its present form was not constructed until 1949. In fact, its versatility was not fully appreciated until after experimental controls were sought for some of the problems under investigation. During the last two years it has been demonstrated before representatives of over fifteen universities and all branches of the military services in six different problem settings.

EFFICIENCY CRITERIA

The efficiency of a discrimination apparatus may be tested in a number of quite different ways. Some of the criteria are:

1. The number of trials which must be given before the simplest problem is learned by a group of representative subjects.

2. The number of minutes (or man-hours) spent per animal in training it to meet the simplest criterion.

3. The permanence and stability of the retention of previously learned responses.

4. The degree and kind of motivation required.

5. Adaptability of the apparatus and technique to a variety of problems, so that the animal can make one previously learned simple reaction to a wide variety of situations.

6. The number of problems which can be investigated simultaneously.

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[1] The apparatus described in this paper represents the combined ideas and labor of a number of individuals in the Department of Experimental Psychology. M/Sgt N. L. Ehrhart, S/Sgt. D. H. Feitz, A/1C R. S. Massar, and A/1C Harvey B. Anderson were the principal contributors.

So far as developing methods of handling the animals was concerned, A/1C R. S. Massar, A/1C G. H. Rothschild, A/3C R. E. Nye, and A/3C H. L. Perry were primarily responsible.

The applicability of probability theorems has been discussed with a number of individuals: Dr. R. B. Payne of the USAF School of Aviation Medicine, Dr. F. J. Adams and Dr. H. F. Bright of the University of Texas, and Dr. S. J. Kaplan of the USAF SAM Primate Laboratory have all helped to clarify these principles. The probability data were computed by 2d Lt. B. B. Cobb, and 2d Lt. E. W. Moore checked the experimental design.

The views expressed herein are those of the author and do not necessarily represent those of the Department of the Air Force.

7. Suitability of the response to a number of animal species.

8. The extent to which the attention of the subject may be directed to the pertinent points of the problem.

9. Ease with which various elements of the total problem may be isolated for control.

10. Reproducibility of experimental findings in other laboratories.

11. Freedom from possibility of gross methodological and scoring errors on the part of the experimenter.

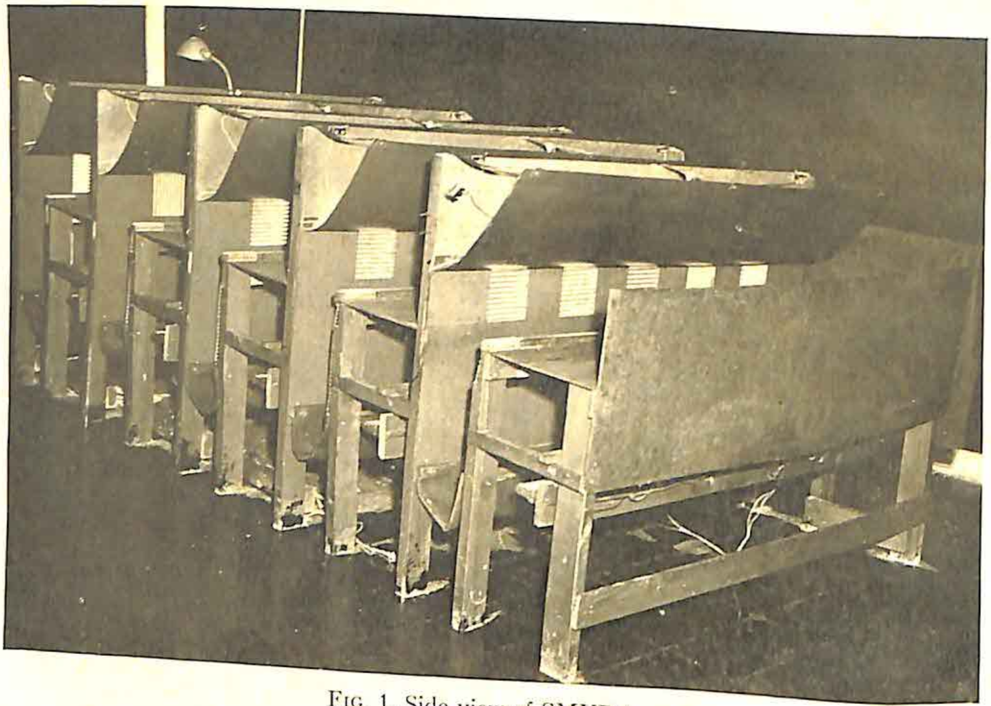

FIG. 1. Side view of SMVDA

12. The statistical sensitivity, reliability, and validity of the results obtained.

DESCRIPTION OF APPARATUS

The present SMVDA (Serial Multiple Visual Discrimination Apparatus) merely puts five of the five-choice multiple units in a row so that now the rats have to jump through the correct aperture in each of five platforms in order to get a single bite of food. The more important additions to the SMVDA not used on the earlier multiple apparatus were:

1. Wire ladders reaching from the apron beneath the stimulus openings up to the top of the jumping platform. Thus, the rat did not need to be handled after an error. When it fell into the apron, it ran to one end or the other and climbed up the wire ladder to the top of the jumping platform.

2. The addition of a battery of six timers and a stepping switch arranged so that as the animal jumped through the positive stimulus cards, it automatically measured the period that it had spent on each platform and on the total apparatus.

The construction details and pictures are presented in a USAF project report (3).

VERSATILITY

In its simplest form, the SMVDA can be arranged so that two stimulus cards can always be presented in the same two holes of each platform. In the interest of equalizing distances from the end of the platform and of intercard distances, holes 2 and 4 will probably be chosen for presentation of the positive and negative stimuli. Under these conditions, with holes 1, 3, and 5 blacked out, the apparatus is a serial two-choice discrimination design. Under these conditions, if the jump to any one card is an error, all the rat has to do is run back up the ladder and jump at the other card. The rats quickly learn this "alternation" and do not pay as much attention to the crucial part of the discrimination problem.

The efficiency of this apparatus in a two-choice setting is greatly improved and the animals' attention is directed to the problem more readily if the same two stimulus cards are presented from the very start of the training process in each of the possible pairs of apertures. There are ten such pairings for the five apertures of each of the five platforms. Since the total stimulus configuration is changed if the position of the positive and negative card is reversed, then there are 20 different geographical (spatial) patterns in which the two stimulus cards can be presented in each of the five platforms, or a possibility of 3,200,000 different stimulus positions available for a single trial sequence. It is believed that this is the reason the rat learns to respond to the essential visual stimulus object in the SMVDA rather than to rely upon kinesthetic patterns.

A simpler form of presentation which keeps the stimulus cards in adjacent apertures would reduce the number of possible pairings to four instead of ten, but by using a table of random numbers to secure randomization of the pairs used, the right-left position of the positive card within each pair, and the side of the jumping platform by means of which the rat is introduced to the problem, very effective discriminations are obtained.

More complex patterns which we have used with success involve:

1. The presentation of the same positive stimulus with the same four identical negative stimuli in each of the five platforms of the apparatus. This is somewhat similar to the problem involving the perception of the one dissimilar object. However, no effective argument has been raised to prove that visual acuity is not fundamental to success in the oddity test. If the extension of the "oddity principle" to five instead of three stimulus objects makes it possible for a rat to choose correctly stimuli which previous investigators have declared to be beneath its visual threshold, then we have merely added an additional refinement to a discrimination apparatus and method.

2. The presentation of a different combination of one positive stimulus with four identical negative stimuli in each of the five platforms. For example, in an acuity problem the first platform would contain one card with vertical and four cards with horizontal black and white stripes, each 20 mm. in width. The second platform would have cards with 15-mm. striae, the third platform 10-mm. striae, etc. The use of a latin-square design for placement of the positive stimulus guarantees that the same numbered opening will be used but once for the positive stimulus in any series of five trials, and that the sequence of openings on a trial run through the apparatus will not be duplicated in any five-trial series. The use of additional latin squares will rule out the possibility that the rat can ever learn the correct spatial order of the responses. With this method five different levels of visual discrimination can be checked on one trial run.

3. A presentation of five different stimuli in each of the five platforms. For example, in a brightness discrimination, the first platform would have a set of five different gray cards, the second platform a new set of five different gray cards that were a little darker than the first, etc. On each of the five platforms the rats were required to jump to the brightest card. As they progressed through the five platforms on any one trial, they were eventually jumping correctly and positively to stimulus values which on an earlier platform had been negative. Five different levels of brightness threshold discrimination have been investigated simultaneously in this way. The dark to light order gives different discrimination times from those obtained when the same cards are presented in the light to dark order.

So far as acuity is concerned, we have also presented a positive vertically striped card of a certain width with four cards having different widths of horizontal stripes on each platform. As long as the width of the vertical stripes on the positive card are above the rats' threshold, they will jump to it in this combination.

It is also possible to get an indirect measurement of brightness discrimination from rats trained only on an acuity problem merely by replacing the black and white striped cards with cards on which the stripes are made of different shades of gray. When the animals are no longer able to stay above the required accuracy level in discriminating between the vertically and horizontally striped cards (the width of stripe having remained the same), the breakdown must be due to a failure to perceive the difference in brightness of the stripes. If it were not for the possibility that the rat would still jump to a card with striations so close as to be beneath its threshold merely because it could see the others and therefore avoid them, it might be possible to train it to jump to the card with the smallest stripes (all vertical). It has been possible to get a positive transfer from vertical alternate black and white stripes to a single vertical stripe on the contrasting background in less than five trials. (A 20-mm. vertical black stripe on a white card, or a 20-mm. vertical white stripe on a black card was discriminated from a 20-mm. horizontal stripe with the same backgrounds.)

4. It has been possible to use the SMVDA for tuitional controls. For example, on the first two platforms any four of the openings are blocked out and the positive stimulus presented in the fifth one. The rat jumps to this one card (vertical 15-mm. stripes) on platforms 1 and 2 and immediately finds five different stimuli (vertical 20-, 15-, 10-, 7-, and 5-mm. stripes) confronting it on the third platform. It must now jump to the one of the five cards that most closely approaches the width of the stripes on the single stimulus card just reacted to. Platform 4 would contain a single reinforcing card, and the fifth platform would again have five similar cards with vertical stripes of different widths. The use of guided training such as this has proven to be the most efficient method for establishing visual discriminations.

A "help" is recorded whenever, after the rat is placed on the apparatus, any overt behavior on the part of the experimenter either initiates activity in the rat or helps direct it toward the stimuli to be discriminated. A help is usually a motivational device, although in certain extremes it may result in actually placing the rat in front of the positive stimulus and forcing it to jump. Letting the rat smell the food dish, replacing it on the bottom of the ladder leading to the jumping platform, tapping either the apparatus or the rat's tail, moving the rat on the apparatus or placing it between or in front of the stimuli to be discriminated are all considered as helps. On the other hand, in "guided training" the apparatus is set up in such a way that the animal sees only the positive stimulus and responds to it without any urging by the experimenter. In this case, one positive stimulus is exposed with four black cards. Guided training of this kind is not maximally effective until after the rat has been oriented to the apparatus and the experimental routines, and has learned its first discrimination problem with the aid of helps. If the rat failed to jump in a specified time limit in a guided setting, then the expericontrol for it. However, on the early training trials the use of the latin square does help eliminate position habits and guarantees attention to a stimulus pattern which is constantly changing its position in space.

The fact remains that the speed of a single trial was always increased whenever any regularity appeared in the trial series. For example, if the positive stimulus card was exposed on each of the successive platforms in holes 1, 2, 3, 4, and 5, the time for that trial would be less than when they were placed in holes 3, 1, 5, 2, 4. It is obvious that the second trial order forced the animal to run farther in order to see all the positive stimulus cards, but the time difference is not due solely to the distance traversed.

The treatment of errors also has a bearing on probability computation. In either the two- or the five-choice apparatus, if the positive stimulus card is kept in place until the rat jumps to it, the number of errors (jumps to the negative stimulus cards) per trial is a variable factor. In this case "trial" means "all the jumps necessary to get to the goal." In the two-choice apparatus the rat quickly learns that if its first jump was unsuccessful, all that is necessary is to jump to the other card and it will be fed. However, on the five-choice apparatus when the rat makes an error, there is still only one chance out of four that it will be correct on the next jump to the same platform, and this probability applies only if we assume that the rat remembers each of its previous errors and avoids that aperture on the next jump. Under this reasoning, the rat is entitled to make 20 errors in a single run through the SMVDA before it has reached a chance level on the discrimination.

If only the first unaided jump on each platform is counted, but the rat is still required to rectify each mistake and complete a successful jump to the positive card on each of the five platforms in a single trial run through the apparatus, then the rat has the advantage of a large number of training jumps (corrections) to the various stimulus cards which are not reflected in the data. If a time limit is specified for each discrimination, then the most severe condition would count only the first unaided correct responses out of the total number of opportunities where a failure to jump would be counted the same as an error. Next in order of difficulty, and perhaps the most reasonable measure, is the number of jumps which were correct out of the total number of first responses completed within the designated time limit. This method has the additional advantage of eliminating unwanted motivational factors. For example, it did not lower the animal's visual-acuity score merely because the animal was too sick or excited to make the effort to jump. More lenient still is the number of correct jumps out of the total number of unaided jumps made within a specified time limit.

It is instructive to compare what happens after errors are made on the SMVDA and the two-choice apparatus. For example, suppose that a rat made a successful unaided first jump to the positive stimulus cards on platforms 2, 4, and 5. It was incorrect on the first jump to platform 1 (correct on the second jump), and made an error on the first jump to platform 3, which was corrected on the next jump. After each of these errors, if the rat fell into the apron beneath the stimulus screen, it had to climb up the ladder at the extreme end of the jumping platform and run its complete length in order to observe all the stimulus cards. If we apply the strict interpretation, the cumulative probability of three or more unaided correct jumps on five platforms in a single trial is .057. Under the more lenient interpretation, five out of seven jumps correct in a single trial gives a probability of .0046.

With the two-choice apparatus, the rat that made an error was placed back on the jumping platform where it was equidistant between the two stimulus cards. All the rat had to do was to jump to the "other" card and it would get to food. (Lashley reports that on some of the stimulus reversal orders he studied, it was possible for a rat with an alternation habit to get 70 per cent of the jumps correct by chance.) Under the strict interpretation, three or more unaided correct responses out of five would have a probability of .50 while five or more out of seven correct jumps would be .22.

A comparison of the probability data obtained on this serial multiple apparatus as opposed to that obtained with the usual single-unit two-choice apparatus is presented in Tables 1 and 2.

Inasmuch as motivation has always been considered an important factor in all animal work, it is desirable to get as many performance data per unit of reward as possible. The data for trials in Table 1 give the probability of getting successive correct responses per unit of reward. The SMVDA is markedly superior to the single-unit two-choice apparatus whenever motivation is an issue. This is the principal contribution of the serial arrangement of the apparatus.

TABLE 1
Probability of Getting a Specified Number of Successive Correct Discriminations

CORRECT JUMPS	APPARATUS	
	Single-Unit Two-Choice	Single-Unit Five Choice
1	.50	.20
5	.03	.0003
10	.0009	.0000001
25	.000000029	.000000000000000003
CORRECT TRIALS	Single-Unit Two-Choice	SMVDA
1	.50	.0003
5	.03	.000000000000000003

TABLE 2
Cumulative Probability Data and Per Cent Correct at Various Levels

TRIALS	NUMBER CORRECT	UNAIDED FIRST JUMPS	CUM. PROB.	PER CENT CORRECT
SMVDA				
1	4 out of	5	.007	80
2	6 “ “	10	.006	60
3	8 “ “	15	.004	53
4	9 “ “	20	.010	45
5	11 “ “	25	.006	44
Single-Unit Two-Choice				
10	9 ” ”	10	.010	90

On the usual day's run on simple problems where the rats were given only five trials on the SMVDA with the latin-square design (rat got five opportunities to eat during the day's runs), it had to make only 11 unaided correct discriminations out of 25 to be working at better than the .01 level of confidence. On all threshold studies with this apparatus and method, acceptable probability data (.05) can be secured when the rats make only 9 correct discriminations out of 25.

SAMPLE EXPERIMENTAL DESIGN

The possibilities of the apparatus may be fully utilized in the following type of experimental design. We wish to investigate the effect of two different amounts of some variable (drug, radiation dose, altitude, etc.), upon the ability of two different groups of animals to perform certain tasks. The five tasks chosen might be acuity, brightness, size, and form discriminations, and a multiple-choice task. One problem is presented on each unit of the SMVDA so that the animal in a single trial run makes a response to all five. If the animals are divided into two classifications (male-female, or young-old), the design can be set up according to Table 3.

TABLE 3
Sample Experimental Design

SUBJECT CATEGORY	PROBLEMS	AMOUNT OF RADIATION		
		0 r.	250 r.	500 r.
		Subjects per Cell		
Young	Acuity Brightness Size Form Multiple-Choice	10	10	10
Old	Acuity Brightness Size Form Multiple-Choice	10	10	10

Post radiation effects may be studied by the usual methods of analysis of variance or covariance.

An additional refinement which greatly increases the statistical sensitivity involves the use of a double or triple classification (two or three degrees of learning or age of habit on each of the five types of problem). However, it should be noted that this sophisticated experimental design will lose much of its value unless the five separate problems used are sensitive and valid measures of the animal's performance. If all the problems were exceptionally easy ones, the statistical design alone might not reveal the small differences which could be brought about by radiation. What is needed first is a thorough analysis of the animal's reaction possibilities to near-threshold stimuli in order that the most sensitive experimental measures of the animal's various capacities can then be combined with the most sensitive statistical techniques to reveal any possible change due to the experimental variable. The search for a single threshold is likely to consume more time than will be necessary to carry out the definitive studies on all five problems once the proper range of difficulty has been established on the apparatus.

PRELIMINARY FINDINGS

With the .01 level of confidence as the criterion of a discrimination, albino rats have discriminated 1-mm. black and white striae, a .5-mm. white line on black, and a 1-mm. black line on white cards. They also discriminated a 2.5-mm. black line bisecting 50- and 40-mm. white squares, a 5-mm. black line bisecting a 15-mm. square, and a single vertical 1- by 20-mm. white line from a horizontal. In all cases the jumping distance was 21 cm. These data are superior to those reported for pigmented rats.

Twenty-two different brightness ratios secured with gray papers were explored under the same levels of illuminance. In general, holding contrast constant, the accuracy of the discrimination was reduced as the reflectance was increased. The use of a 10-mm.-wide vertical stripe against a 6- by 6-in. ground where the brightness of both was systematically varied eliminated some of the problems encountered in the use of solid areas.

Using only one unit of the apparatus, rats have discriminated perfectly between 50 different perceptual symbols during a single experimental period. Presenting the positive symbols in a new serial order and paired with different (and in some cases, completely strange symbols) did not affect the accuracy of the response. After only five guided trials, they could pick out this one symbol from a panel of five strange symbols.

Training to one card with vertical striae exposed with four black cards in the units of the SMVDA resulted in immediate and perfect positive transfer when four horizontal striae replaced the black cards. An additional week's testing on this problem was followed by the selection of five new and strange symbols upon their first presentation with the four negative horizontal striae in each unit.

Each of these studies will appear as separate articles in the future.

SUMMARY AND CONCLUSIONS

An apparatus and method have been described which make possible quick and accurate visual threshold determinations at a level of confidence never approached before. This extra margin of speed and safety is particularly important when it becomes necessary to evaluate the potential hazards of various agents upon human beings by extrapolation from animal *S*s.

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EFFECT OF A SECONDARY REINFORCER ON THE PRIMARY HUNGER DRIVE

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Hull's (2) description of Primary Reinforcement in Postulate III stresses the importance of the drive stimulus and the reduction of this drive stimulus in the formation of *S-R* connections. The drive stimulus concept is carried into Corollary i, Secondary Motivation, wherein it is stated that a neutral stimulus acquires the capacity to bring about the drive stimulus. Presumably this is the same stimulus that is produced by the primary need state. Thus a very intimate relationship, in fact one of identity, is presumed to exist between the primary drive stimulus and the secondary drive stimulus. In Corollary ii, Secondary Reinforcement, reference to the drive stimulus is omitted, and there is no clear statement to the effect that the secondary reinforcer either reduces or fails to reduce the drive state. However, his use of the phrase "reinforcing state of affairs, whether primary or secondary" would seem to imply that the secondary reinforcer serves to reduce the drive. The formulation in Postulate III would, therefore, seem to predict that the occurrence of secondary reinforcement would modify the primary drive state. This modification would seem to be in the direction of reducing the primary drive.

The position that learned motive-incentive states reduce the primary drive is not unique to Hull. Tolman (4) includes as one of his six types of learning the concept of equivalence belief learning, which is precisely of this nature. The psychoanalytic concept of sublimation seems also to make a similar assumption.

To test the hypothesis that the occurrence of secondary reinforcement affects the primary drive, Simon, Wickens, Brown, and Pennock (3) trained albino rats to press a bar in a water box. Each bar press was reinforced by allowing the animals, under thirst drive, to drink 4 min. from a water tube inserted into the box. When the bar was pressed, the animals were stimulated with a light, buzzer, and the sight of the drinking tube; all were considered secondary reinforcers. One group of animals underwent habit extinction without the customary secondary reinforcers, whereas the control groups were stimulated with the secondary reinforcers during extinction. No reliable difference was found between the groups in the amount of water consumption, tested immediately after the extinction trials. If a secondary reinforcer did affect or partially satisfy the primary drive, the animals stimulated with the customary secondary reinforcers would be expected to drink less than the group not so stimulated.

The purpose of the present study was essentially to repeat this experiment, utilizing a different drive state. Specific departures from the earlier study were the use of hunger drive, a test under high and low drive, and a final check to see if the stimulus so defined was actually a secondary reinforcer.

Stated generally, the purpose of the present experiment as in the earlier one was to determine whether a secondary reinforcer had any observable effect on the primary drive.

METHOD

Apparatus

The apparatus was a modified Skinner box, double-walled and insulated. When a bar inside the box was depressed, a magnetic release mechanism emitting a sharp click delivered one pellet of food. When the current output of a transformer was decreased, a bar press would result in neither click nor food; however, a magnetic counter outside of the box would cumulatively record the number of bar presses.

Procedure

Pretraining. Records of individual daily food consumption were obtained for a ten-day period. Two groups of animals were formed by equating for sex and quantity of food consumed during the last two days of the ten-day period. The mean consumption for one group, called group A, was 8.0 gm. and the mean for the other, called group B, was 8.1. During this period the animals were also trained to press the bar in the modified Skinner box for food reinforcement. Each bar press allowed one pellet of food to drop into the food tray.

For all pretraining and the high-drive test days the animals were deprived of food for 22 hr. and allowed a 2-hr. eating period in an individual cage after each experimental session. In each training session the animals remained in the box for either a maximum of 15 reinforcements or 1 hr. This training continued until each animal had 75 reinforcements paired with the sharp click of the delivery mechanisms.

Test days. On the first test day the animals were given 20 extinction trials, group A with the customary secondary reinforcer, click, whereas the eight animals in group B were extinguished without the secondary reinforcer. Immediately after the extinction trials each animal was placed in an eating cage and allowed to eat for the usual 2-hr. period. On the next three days all animals were given 15 reinforced trials a day to reinstate the habit. The extinction procedure was repeated with the procedure for group A and B reversed. Now group B received the customary click and group A extinguished without the click.

The complete procedure stated above was repeated with the animals under a low-drive state of 6-hr. food deprivation.

A final check was made to see if the click could be considered a secondary reinforcer. Again, the habit was reinstated with 15 reinforcements a day for a three-day period. The animals were randomly separated into two groups, eight animals in each group. The bar-pressing habit was then extinguished for the two groups, one with the click and the other without the click. The criterion for extinction was a 5-min. period with no bar presses.

TABLE 1

Food Consumption in Grams for the Equating Period and Test Days

GROUPS	GROUP A		GROUP B	
	Mean	*SD*	Mean	*SD*
High Drive				
Test Day 1......	*7.6**	1.2	7.8	2.1
Test Day 2......	7.4	1.5	*8.3*	1.7
Low Drive				
Test Day 1......	*6.0*	1.3	6.3	1.8
Test Day 2......	5.3	2.7	*5.7*	1.9

* The italicized score refers to the group which underwent extinction with the secondary reinforcer present.

RESULTS

The mean quantity of food eaten by each group during the two tests under high and low drive is shown in Table 1.

There was no significant difference (by *t* test for related means) between groups during the equating period or on the test days, either under high or low drive. Amount eaten for odd-even days during the equating period correlated .81 ± .09. Correlation coefficients between the quantity eaten during the equating period and the two high-drive test days were .54 and .57. The probability of obtaining the above two correlations by chance is .05.

Animals that underwent extinction of the bar-pressing habit with the click pressed the bar 37 per cent more times than the group extinguishing without the click. The difference between the two groups was significant (by *t* test) beyond the .01 level. In a similar study, Bugelski (1) found an extinction differential of 30 per cent favoring the click or secondary-reinforcement group.

DISCUSSION

The study by Simon, Wickens, Brown, and Pennock failed to find any effect upon the primary thirst drive as a result of the receipt of secondary reinforcement. A similar group of negative findings occurs in the present experiment. In the earlier experiment two separate tests and in the present experiment four separate tests were employed, and in no instance did the group which received secondary reinforcement differ significantly from the group which did not receive it. Both experiments employed the technique of alternating groups, so that each group served under each condition. It is unlikely that the results can be attributed to the chance assignment of heavy drinkers or eaters to a particular group.

At least as measured by the present technique, the two experiments together fail completely to support the view that the occurrence of secondary reinforcement serves to decrease or increase the primary drive state. Inasmuch as in the high-drive test situations in this and also the Simon experiment the means of the experimental groups were lower than the means of the controls, further investigation is warranted employing different testing or training procedures.

SUMMARY

This experiment was designed to test the hypothesis that the occurrence of secondary reinforcement affects the magnitude of the primary drive as measured by consummatory behavior.

1. Sixteen rats were conditioned in a Skinner box with food as a reward and a click associated with the delivery of food.
2. Half the animals were given 20 extinction trials with click present and half without.
3. Immediately afterward food consumption was measured in a situation to which the animals had previously become habituated.
4. The test situation was repeated after reconditioning with groups reversed.

5. Test pairs were given under primary drive states of 22-hr. and 6-hr. deprivation.

6. In none of the four test situations is there any statistical evidence that the groups differ from each other.

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THE EFFECT OF VARIABLE FOOD REINFORCEMENT ON THE STRENGTH OF A SECONDARY REWARD

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Secondary rewards like money or social approval are usually assumed to be of major importance in the motivational structure of human beings, yet laboratory experiments in which previously neutral cues, such as a poker chip (3), a click (2), or a goal box (10), have been associated with primary food reward have not succeeded in establishing such secondary rewards with the kind of strength and persistence that seems to be required for the understanding of human motives. Thus, at the human level secondary rewards at times seem more powerful than primary ones, as in the case of martyrs, yet it has been difficult to establish a parallel phenomenon experimentally. It is just this problem that appears to have led Allport (1) to formulate his well-known doctrine of functional autonomy, which states that motives eventually come to function independently of their biological origin.

A useful approach to the problem is to consider, as McClelland has in another connection (9), what conditions are necessary for an association, once learned, to be unlearned. One such obvious condition is that the organism must be able to distinguish between acquisition and extinction. In the normal extinction situation, of which secondary-reward extinction is a case in point, this is easy. The animal is first fed in a distinctive reward box (acquisition) and then is not fed when it enters the same box (extinction) (see 10). In some situations, however, the discrimination between the acquisition cues and extinction cues is not so easy for the animal. Thus, in avoidance training the animal normally has no way of knowing that extinction has begun, for it is making a response which prevents its discovering that the shock has been omitted.

A particular condition which makes it difficult for the organism to determine that extinction has begun is the nonspecificity of the original learning. The more general the association formed during original learning, i.e., the more variable the conditions under which it is formed, or the more cues built into the association, the harder it should be to establish conditions which should lead to extinction of the original association through nonreinforcement. One of the characteristic features of learning in life situations is this very generality; it is a rare child who is consistently reinforced for making a specific response on every occasion. So the present experiment was designed to establish a secondary-reinforcement situation which was more nearly like the variable, uncontrolled training which occurs naturally and to test for the persistence and strength of a secondary reward acquired under these conditions as contrasted with its strength when acquired under the more usual laboratory conditions of regular systematic association with primary reward.

METHOD

Apparatus and Subjects

The apparatus used in this experiment is diagrammed in Figure 1. It consisted of a circular goal alley (cf. 4) constructed of aluminum and with a smooth wood floor. It was 5 in. high, 5 in. wide, and had a circumference at its center of 72 in. It was open at one point to permit entry of the rat either via the entry box used during training or the T maze used during testing. The entry box consisted of a narrow compartment with an inclined runway leading down to a sliding door which could be lifted to permit the rat to enter the alley. The T maze illustrated by dotted lines in Figure 1 replaced the entry box during testing. It consisted of one section 39 in. long which formed the bar of the T. The other section was 18 in. in length and led to the circular goal alley via a raised wooden hurdle, 3 in. high, over which the rat had to squeeze in order to enter the goal alley. The sections of the T maze had smooth wooden floors 3½ in. wide and wooden walls 6½ in. high. The rats were placed in the T maze at the section marked *S* in Figure 1, and lines were drawn on the floor of the maze at *a*, *b*, and *c* to facilitate the recording of errors. The rat was recorded as having crossed one of these lines if both its front feet were over it, and as having entered the goal alley only if all four feet were over the barrier at the entrance. All parts of the apparatus were covered with hinged wire-mesh sections which were movable to permit easy access by *E*.

The animals used were 44 experimentally naive male albino rats, three to four months old.

Procedure

Habituation—three days. The animals were isolated in individual wire cages in which there was plenty of water at all times. They were then fed once every 24 hr., for three consecutive days, by *E*, who picked up and handled the animals on eight different occasions on each day, offering them food in the form of a pellet of wet mash each time. This insured the association between handling and being fed, inasmuch as this combination of events occurred at least 24 times before actual training began. It also served as a means of eliminating previous to training any animals that would not readily adapt themselves to being handled by *E*. The feeding was done at the same hour of the day, approximately, at which the subsequent training and testing for that particular rat was to take place.

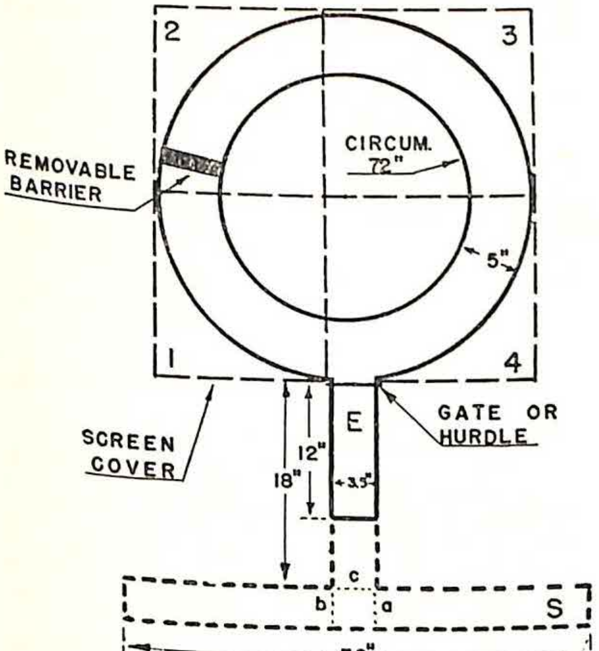

FIG. 1. Diagram of the apparatus. Solid lines show the arrangement during training, broken lines during extinction. During training the animals were placed at *E*, during extinction at *S*.

Training—three days. For the specific-reinforcement group a pellet of wet mash was placed in front of the barrier located just beyond the end of section 1 of the circular goal alley, as illustrated in Figure 1. The rat was placed in the entry box and the gate lifted. The fact that the floor of the entry box was inclined tended to make the animal slide down and out into the goal alley. The time between the moment when the rat left the entry box and started to eat the food was recorded by a stop watch in *E*'s hand and was considered a measure of latency or running time. When the animal finished the pellet, it was removed from the goal alley to a waiting cage, which was not the same as the home cage, where it was kept for 20 ± 5 sec. before being returned to the entry box for the next trial. Each of the 11 rats in this group received eight such reinforcement training trials on three consecutive days.

A control group of 11 animals was run under precisely the same procedure except that they never were fed in the goal alley. Instead, they were allowed to wander in the goal alley for an amount of time approximately equal to the time spent there by the rewarded rats on each of the three days of training. Because the amount of time spent in the alley by the rewarded rats decreased from day to day as they learned to find the food, the amount of time the control rats were left in the goal alley was decreased from 90 sec. for each trial on day 1, to 60 sec. on day 2, to 30 sec. on day 3. This was designed to include running time and time to eat the food pellet. The control animals were fed eight pellets on each of the training days according to exactly the same procedure as had been used during habituation. That is, after the training session each rat was removed to its home cage and fed approximately ½ hr. after the last rat in the group being run had completed the training trials. The purpose of this was to dissociate feeding as much as possible from the exploration of the circular goal alley.

For the general-reinforcement group no barrier was present, and the food pellets were made available in each of the four sections of the goal alley twice during the eight reinforcement trials but in a randomized fashion. Furthermore, half the time the pellet was placed on the floor of the alley so that the rat could run around until it found the food, and half the time it received the pellet only if it stopped in the "correct" section. If these two types of reinforcement are labeled *R* (for running) and *S* (for stopping), and if the numbers *1, 2, 3, 4* refer to sections of the goal alley as in Figure 1, then the types of reinforcements were distributed as follows on the eight trials for each of the three consecutive days of training: *R*1, *S*3, *R*2, *S*4, *S*1, *R*3, *R*4, *S*2. It was hoped that in this way the animals in this group would be prevented from associating any particular response (turning left or right, running or stopping), or any particular time delay, or any particular place in the goal alley with food reinforcement. In contrast to this, the animals that had received specific reinforcement always found food in the same place and could reach it in approximately the same amount of time by turning left and running directly to it. Aside from these differences in the reinforcement procedure, the animals in the two groups were handled in exactly the same way.

A control group of 11 rats was also run for the general-reinforcement procedure. They did not receive any reinforcement in the goal alley, and unlike the conditions for specific control group there was no barrier in the goal alley. Furthermore, the time that these control animals were allowed to stay in the goal alley on each of the eight trials was determined by the approximate amount of time spent by the generally reinforced animals on comparable trials. Specifically, this meant that they were allowed to spend 90 sec. in the goal alley on all trials during the first day of training, 60 sec. on the running trials and 90 sec. on the stopping trials during the second day, and 30 sec.

on the running trials and 60 sec. on the stopping trials during the third day.

Testing—one day. In testing, the entry box was replaced for all rats by the T maze, and each animal was placed in Section *S*. It was hoped that by introducing a choice point, some measure could be obtained of the extent to which a secondary reward would produce new learning. It was impossible to use a simple right-left discrimination without causing positive or negative transfer for the specifically reinforced rats which during training had learned to turn left. Consequently, the choice between going straight ahead and turning right was introduced as being intermediate between positive and negative transfer. The time taken by the rat to cross the barrier into the goal alley was recorded beginning at the moment the animal was placed in Section *S*. After it crossed the hurdle, it was left to explore the goal alley for 15 sec. before being removed to the waiting cage, where it remained for 20 ± 5 sec. before the next extinction trial, as in the training procedure. There was no food in the goal alley at any time in the test series. The barrier was left in place for those animals that had experienced it during training. Each animal was given 25 extinction trials. Because many rats did not cross the hurdle into the goal alley on one or more of the extinction trials, an arbitrary upper limit for the duration of each trial was set at 120 sec., at which point the animal was removed to the waiting cage to prepare for the next trial. Inasmuch as the animals could run freely in the T maze, retracing errors were possible; but no errors were counted after the animal had once entered the goal area, even though it might return immediately to the T section.

RESULTS

Training

The behavior of the rats on the three days of training is of interest for two reasons: to determine whether the groups of rats are equated initially in ability, and to analyze just what the animals that had received general reinforcement had learned as compared with those that received specific reinforcement. Table 1 supplies data which are relevant to both problems.

TABLE 1

Mean and Median Running Times in Seconds for General and Specific Reinforcement Groups at the Beginning and End of Training

TYPE OF REINFORCEMENT	*N*	DAY 1 TRIALS 1 AND 3 COMBINED			DAY 3					
					TRIAL 23			TRIAL 24		
		Mean	*SD*	Median	Mean	*SD*	Median	Mean	*SD*	Median
Specific	11	66.9	30.5	52.5	1.56	.56	1.00*	1.27	.45	1.00*
General	11	64.5	46.8	57.0	8.36†	8.14	6.00	18.27†	7.71	18.00
Difference		2.4		−4.5	−6.80	7.58	−5.00	−17.00	7.26	−17.00
$\sigma_{\text{diff.}}$					2.59	1.74		2.44	1.64	
CR					2.63	4.36		6.97	4.43	
p					<.05	<.01		<.01	<.01	

* Mode since more than half the rats ran in 1 sec.

† Reinforcement for running on trial 23, for stopping on trial 24.

On each training day rats had been run under both types of reinforcement so that any differences due to shipment, changes in experimental handling, etc. would be equalized for the two reinforcement groups. The success of this approach is indicated to some extent by the first column in Table 1, which shows the mean running time on trials 1 and 3 for both groups on the first day of training before the different types of training could have had much effect. It had been arranged so that the food reward for the general group was placed in nearly the same position on the first trial of training as it was for the specific group (i.e., in section 1 to the left of the entrance into the goal alley). Unfortunately comparison on this trial alone proved impractical because of the tremendous individual differences in the amount of time the rats took in exploring the circular alley before eating. Consequently, the running times on trial 3 were averaged in to provide a more stable figure for each rat. On this trial the rats in the general-reinforcement group found the food to the left of the entrance but a little farther along (in section 2). They had also had an intervening trial in which they had been reinforced for stopping in section 3, as compared with the specific-group rats, which were always reinforced for running to food in front of the barrier at the end of section 1. In spite of these differences the figures in Table 1 show that the running times for these two trials are about the same on the average for the two groups of animals. Although this is not an ideal test of the initial ability of the two groups, it does indicate the absence of any marked group differences which might have arisen by chance in selecting the animals for inclusion in the two groups.

As to whether each group of animals learned anything, it is fairly apparent that both groups improved markedly from the first to the last training trials. The great variability in running times on the initial trials suggested that some measure other than the mean might be preferable for measuring the extent of learning which took place. Consequently, the mean number of running times on a given day meeting or surpassing a given criterion was computed, following a technique used by V. Sheffield (11). In this case the criterion chosen was the median running time (12.6 sec.) for both reinforcement groups on all three days (24 trials). It is possible to count the number of responses which were equal to or faster than this criterion for each group on each day and to demonstrate that the group which received specific-reinforcement training showed significantly more fast running times on each of the three training days than the variably reinforced group. The same type of analysis applied to gains from day 1 to day 3 shows that both the specific and general groups showed increases in the number of fast running times which are significant well beyond the .01 level (CR's = 9.63 and 5.98, respectively). In other words both groups of rats showed an unmistakable decrease from day 1 to day 3 in the length of time it took them to get food.

Having considered the course of learning, we may now turn our attention to differences in what the animals had learned by the end of training, as illustrated by the data on trials 23 and 24 in Table 1. As far as the animals in the specific-reinforcement group are concerned, the answer is simple. They have learned to turn left (91 per cent of the 22 turns on trials 23 and 24 were left turns as compared with 55 per cent for the general group) to get food in a certain specific place (barrier, floor, wall, and overhead-lighting cues) after a certain specific time delay (1 to 2 sec. for 95 per cent of the running times on trials 23 and 24). For the general group there is no such specificity of response learned (55 per cent left turns, 50 per cent reward for stopping and 50 per cent for running) or of place cues (reinforcement associated equally with all parts of the alley and sometimes with lifting of the screen over the top of the maze), or of delay between entry into the goal alley and receipt of reinforcement. Special attention should be called to the delay factor because it is not only much longer for the general reinforcement group (over-all medians of 19.9 sec. vs. 5.4 sec., trial 23 medians of 6 sec. vs. 1 sec., trial 24 medians of 18 sec. vs. 1 sec.), but it is also significantly more variable on both trials 23 and 24, as Table 1 shows. It seems reasonable to conclude from all this that the association the variably reinforced animals have built up between the goal alley and food must be much more general (based on many more cues) than the association built up by the animals that have received reward after a regular delay, at a particular place, for a particular response.

Testing

On day 4, or the extinction day, a choice point on the way to the goal alley was added in an attempt to get some measures of the relative potency of the two kinds of secondary reward in producing new learning. The attempt was not notably successful. Whether the measure of learning used was *trials* to the first errorless run into the goal alley, *errors* made per completed run into the goal alley, or *number of errorless trials* out of 25, there was little evidence of difference among the two differently trained or control groups, largely because the single choice point provided much too simple a learning problem to show major differences. Also, it was difficult to know just where to stop the measurement. Thus, the generally reinforced animals showed a significant decrease in errors at the 1 per cent level between trials 1 to 10 and trials 11 to 15 whereas neither the specifically trained nor the control animals showed any such drop. But this comparison seems a little arbitrary in view of the fact that on trials 16 to 25 they showed an increase in errors again.

The picture is much more clear-cut when we turn to latency measures or the running times from the start of the test maze to entrance into the goal alley by climbing completely over the barrier. Unfortunately, inasmuch as there were some extinctions (failures to run in 120 sec.) on nearly every one of the 25 trials, mean running times per trial or groups of trials are not very accurate measures of central tendency. To get around this difficulty, two solutions were adopted, one gross measure to show the differences between the two reinforcement groups and the control groups and the other more sensitive measure to show the differences between the two reinforcement groups. The first measure is comparable to that used to measure learning during training and represents the number of response times in the four groups which were at or below 47 sec., which was the over-all median response time for the two reinforcement groups during extinction. By this index the differences are large and significant between each of the reinforcement groups and the two control groups which were combined in the analysis because they gave identical results. The critical ratio for the difference between the mean number of fast running times on the first ten trials for general reinforcement over control was 3.57, $p < .01$; for specific reinforcement over control it was 3.40, $p < .01$. Comparison by the same statistic beyond this point becomes complicated by the fact that the control group showed very few or no such fast running times in the latter trials of extinction. But the evidence is clear-cut that both reinforcement groups show delayed extinction as compared with animals which did not receive any reinforcement training in the goal alley.

Because of the skewed distribution of running times during extinction, it was decided that the best way to handle them for a sensitive analysis of differences between the two reinforcement groups was to convert them into log running times. The mean log running times were computed for each extinction trial for each group, plotted in Figure 2, and tested for significance of linear regression. For the specific-reinforcement group, linear regression (here represented by increasingly slower log running times) contributes significantly to the variance ($F = 22.3$, $p < .01$), but for the general-reinforcement group, linear-regression variance is not significant ($F = .36$, $p > .50$), nor is there significant curvilinear regression as is suggested by the slight decrease in running time followed by an increase. This suggests that the most adequate conclusion that can be drawn from the extinction data for the general-reinforcement group is that as a group they show no significant evidence of extinction in terms of running time whereas the specific group does.

Furthermore the over-all mean difference between the two groups in log running time for all 25 trials is significant ($t = 9.64$, $p < .01$) and the size of the difference shows a significant increase, again as measured by the contribution of linear-regression variance to the variance of the differences ($F = 5.36$, $p < .05$). In short, as far as running time is concerned, the general-reinforcement group is markedly superior to the specific-reinforcement group in resisting extinction, and actually increases its superiority as the number of nonrewarded trials begins to produce extinction of the entering response in the specifically trained animals.

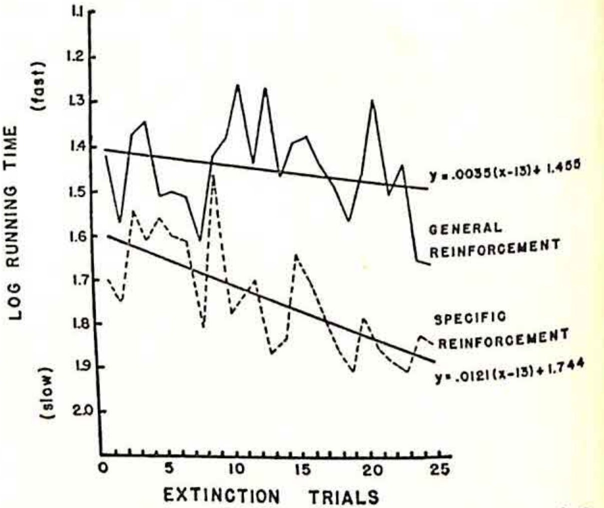

FIG. 2. Mean log running times for each extinction trial for the specific and general reinforcement training groups, showing lines of best fit

The reciprocal of running time or speed was also used as a measure. It gave substantially the same results as reported here except that the curve for the generally reinforced group showed a much more marked increase in running speed in the middle of the extinction series, followed by a drop back to the initial running speed. Since neither the increase nor decrease was significant, the conclusion drawn for the log running time measure seems safest—namely, that the general group shows no significant change in running time during the extinction trials.

DISCUSSION

Both groups of animals that had received reinforcement showed evidence that the goal alley in which they had received food had acquired for them some secondary reward value. The group which had received specific reinforcement behaved during extinction much like animals similarly reinforced in other experiments previously reported (2, 3, 10). That is, during extinction they ran readily into the goal alley much more often than a control group of animals, but by the end of 25 relatively massed extinction trials they showed signs that the secondary reinforcing power of the goal alley had decreased appreciably.

For the animals that had received variable reinforcement, however, the story is quite different. They showed evidence that the goal alley had much greater reward value during extinction than it had for the specifically reinforced animals. They ran into it faster than the latter and by the end of the 25 nonreinforced trials had not yet, as a group, shown significant evidence of extinction. Furthermore, they showed some signs of improved learning in the middle of the nonreinforced trials, as evidenced by a decrease in the number of errors per entry.

This finding appears inconsistent with such previous experiments as Jenkins' (7), in which he reports that the secondary reward value of a neutral stimulus resulting from association with a primary reward decreased markedly as the delay between the neutral stimulus and primary reward increased from 1 to 9 sec. Here, the reverse is true. The goal alley (neutral stimulus) has greater reward value for the variably trained animals which had experienced delays of 6 to 18 sec. before receiving food (primary reward) as contrasted with 1 sec. for the specifically trained animals. Furthermore, probably no particular cue or no particular response was followed by primary reward more than once or twice at the most in the course of the generalized training. Inasmuch as it is commonly assumed that secondary-reward strength, like any habit strength, is a function of the number of primary reinforcements (cf. 5), one might expect less rather than more reward value when the number of reinforcements connected with any particular cue is uniformly low, even if the summation of stimulus and response generalization gradients is taken into account.

The way in which the results are not in line with what would be expected on the basis of such analyses of simple functions suggests a parallel with partial-reinforcement experiments in which less reinforcement has led to a greater delay in extinction. V. Sheffield (11) has explained this phenomenon by pointing out that the change in the stimulus pattern produced by initiating extinction is larger when extinction follows 100 per cent reinforcement than when it follows partial reinforcement. Since the extinction cue pattern resembles the acquisition cue pattern less after 100 per cent reinforcement, the extinction cue pattern should evoke fewer conditioned responses by generalization than if it were more similar to the acquisition cue pattern, as is the case with partial reinforcement. The same argument can be applied here: omission of reinforcement changes the cue pattern less if the original cue pattern is complex or variable than if it is simple and invariant. Therefore, nonreinforcement should produce less decrement in the learned running-into-alley response of the variably reinforced animals than in the same response of the specifically reinforced animals.

This suggests that an important factor influencing the number of trials it takes to extinguish a response is the degree of similarity between the conditions of acquisition and extinction. The less the similarity, the more rapid the extinction, etc. In short, extinction must be considered as a *problem in temporal discrimination* for the animal, and all the factors influencing the ease or difficulty of making discriminations should be influential in determining its course.

Such an interpretation of the extinction problem has two important implications. First, it helps explain why secondary rewards learned under the more variable conditions of everyday life extinguish so slowly. Second, it helps explain why secondary rewards learned early in life, before the young organism has developed the symbolic capacities which make discriminations easier, tend also to be relatively hard to extinguish (cf. 6; 8, p. 116).

SUMMARY

After three days of habituation, four groups of 11 albino rats were given eight trials a day for three days in a circular goal alley. Two of the groups received two different types of food reinforcement on every trial in the goal alley. The two other groups served as controls and received no food in the goal alley. A specific-reinforcement group always found food to the left of the entry into the circular alley in front of a barrier. A general-reinforcement group received food in four different parts of the circular goal alley in a randomized fashion, and sometimes for running to and sometimes for stopping in the appropriate section. On the fourth day, the extinction day, a choice point was added on the way to the circular goal alley, and all four groups were given 25 trials separated by 20-sec. intervals in which no food was present in the goal alley. The following results were obtained:

During Acquisition

1. The specifically reinforced animals showed a large and significant increase in the speed with which they turned left and found the food in front of the barrier.

2. The generally reinforced animals also showed a significant increase in the speed of finding food, but they took longer and displayed greater variability in running time and in responses used to get food than the specifically trained animals.

During Extinction

1. Both groups of reinforced animals ran significantly faster into the goal alley than the nonreinforced control animals, indicating that the goal alley had acquired secondary-reward value for both groups.

2. The generally reinforced animals showed a significant decrease in the number of errors per entry in the middle of the extinction series whereas the specifically reinforced animals did not, suggesting the secondary reward had produced new learning for the former but not for the latter.

3. In terms of time, the generally reinforced animals ran significantly faster into the goal alley throughout the 25 extinction trials than did the specifically reinforced animals. They also did not show significant signs of extinction during the 25 nonreinforced trials, as evidenced by slower running times, whereas the specifically reinforced animals did show extinction by the same measure.

These findings are interpreted as showing that extinction is a function of the ease of discrimination between the cue pattern during reinforcement and the cue pattern during nonreinforcement.

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THE EFFECT OF DRIVE LEVEL ON THE MAZE PERFORMANCE OF THE WHITE RAT[1]

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This experiment was performed to collect data relevant to the following question: Does motivation at the time of training influence habit or merely performance? Methodologically, the previous investigations to which this one is most closely related are those of Finan (4), Kendler (6), MacDuff (7), O'Kelly and Heyer (8), Reynolds (9), Strassburger (10), and Teel (11). The experimental design used in each of these experiments was one in which different groups of *S*s were trained at different drive levels and then tested under equated drive in extinction or relearning. By each of these experimenters, differences in behavior in the *test* situation are taken to mean that differential drive during training produced differences in habit or the amount learned. The absence of such differences means that the effect of motivation is upon performance rather than upon learning. Results of the experiments mentioned above fall about equally into these two categories, indicating the desirability of further research on the question.

METHOD

Apparatus

The apparatus was a 10-unit elevated T maze constructed from planks 2 in. thick by 12 in. high. The starting unit was 30 in. long; other units were 36 in. long. Blind alleys in the maze were 9 in. deep, and the distance between choice points was 18 in. The sequence of correct turns was *LRRLRLLRL*. At the end of the maze was a goal box, into which there extended the nipple of a water bottle attached to the outside of the goal box.

Subjects

The *S*s in the experiment were 40 male albino rats from the colony maintained by Brown University, 60 days old at the beginning of pretraining. Before beginning the experiment, they were blinded and placed in individual living cages. During the whole experiment, they were on an ad libitum supply of food. Motivation in the experimental situation was controlled by manipulating water deprivation.

Procedure

In experiments involving the thirst drive, such variables as temperature and humidity may seriously affect the motivational level of the *S*. For this reason it is desirable to run various groups at as nearly the same time as possible. In this experiment, *S*s in all groups were run early in the evening, and the investigation was performed in two replications. Since the results of the two replications were the same, and since neither humidity nor temperature showed systematic variation during the experiment, both procedure and results will be described as if the experiment had required just one series of sessions.

The *S*s were placed on a 22-hr. drinking schedule two days before pretraining, and kept on it through the pretraining series. Pretraining consisted of 20 trials on a straight runway constructed from three maze units and the same goal box as was used later on in the maze. During pretraining, the *S*s were run under 22 hr. of deprivation and were allowed to drink for 30 sec. in the goal box at the end of each run. Trials were administered at the rate of two a day. After ten such days and 20 trials, running time had decreased to about 5 sec., and group variability was low. At this point training on the maze was begun.

In this training, the *S*s were given 15 trials on the maze, at the rate of one trial a day to eliminate possible complicating effects of drive reduction produced by the administration of reward. During the first ten trials, 20 *S*s were run under 2 hr. of water deprivation and the remaining 20 *S*s were run under 22 hr. of deprivation. The 2-hr. group was allowed access to water continuously except for the 2 hr. immediately preceding the experimental period. The 22-hr. group remained on the same schedule as during pretraining. On each trial, *S* was allowed 45-sec. access to water in the goal box.

After trial 10, the two groups were subdivided and ten *S*s from each group assigned at random to a 2-hr. group and a 22-hr. group. Beginning on the evening following trial 10, each of the four subgroups thus produced was given five more *rewarded* trials in the maze on the one-trial-a-day schedule.

The experimental design, it will be seen, is a 2 × 2 factorial, in which motivation during trials 1 to 10 defines one marginal, and motivation during trials 11 to 15 defines the other. Results from a design of this sort are easily treated by the analysis-of-variance technique. An effect on *habit* is demonstrated if the measures obtained on trials 11 to 15 are significantly different for *S*s trained on trials 1 to 10 under the two degrees of motivation. An effect on *performance* is demonstrated if the same measures are significantly different for *S*s run under the two different levels of motivation on trials 11 to 15. We shall refer to the four experimental groups in this design in terms of the number of hours of deprivation obtaining in the two phases of the experiment. For example, group 22–2 is the group run first under 22 hr. of water deprivation and then shifted to 2 hr. of deprivation. Group 22–22 is that which received all of its trials under 22 hr. of deprivation. The other two groups will be called group 2–22 and group 2–2. Our main interest is in the performance of these four groups on the last five trials of training, in terms of number of errors and amount of time accumulated in each maze run.

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[1] This report is a description of a portion of the senior author's Master's thesis, done at Brown University under the joint direction of the other two authors. The junior author (G. A. K.) assumes the responsibility for the interpretation of the results presented in this paper.

TABLE 1

Analysis of Variance Performed on Mean Error Score and on Mean Log Running Time during Trials 11 to 15 in the Maze

SOURCE OF VARIATION	*df*	ERROR SCORES			TIME SCORES		
		Sum of Squares	Mean Square	*F**	Sum of Squares	Mean Square	*F**
Motivation trials 1–10	1	2.03	2.03	3.08	0.00	0.00	0.00
Motivation trials 11–15	1	2.03	2.03	3.08	1.02	1.02	51.00
Interaction	1	0.07	0.07	0.11	0.06	0.06	3.00
Within groups (error)	36	23.91	0.66	—	0.60	0.02	—

* The *F* ratio required for significance at the .05 level is 4.17; for significance at the .001 level, 13.29.

RESULTS

Let us consider error scores first. If we use as a measure of performance mean number of errors per trial for each *S* on trials 11 to 15, averages are 0.9, 0.9, 1.2, and 0.4 errors for groups 22–22, 2–2, 22–2, and 2–22, respectively. Differences assignable to level of motivation either during the first ten trials or the last five trials fail to reach significance at the .05 level. The analysis of variance on which this statement is based is presented in the left-hand portion of Table 1. Learning curves for the four groups are nearly identical. There is, in short, no evidence that the number of errors is related to strength of motivation at *any* point in learning.

The time scores show quite a different picture. Learning curves for the logarithm of this measure are presented in Figure 1. Note that the groups are clearly different from approximately trial 3 on. Also note that, with the motivational change introduced on trial 11, performance immediately slows up for group 22–2, and that a decrease in the time measure occurs for group 2–22 on trial 12. The fact that the response of this latter group to the change in deprivation is delayed for one trial may represent a residual effect of ten days of nearly continuous free access to water. Finally, observe that the speed of maze traversal seems to depend almost entirely upon motivation during the trials when it is measured. Mean log time scores for groups 2–2, 22–2, 22–22, and 2–22 are 1.66 sec., 1.74 sec., 1.34 sec., and 1.42 sec., respectively. This last fact argues against the idea that drive level during learning has anything to do with the amount learned and is supported by the analysis of variance presented in the right-hand portion of Table 1. The results of this analysis show that the only significant experimental contribution to variability is that from the motivational level at the time the measures used in the analysis were obtained.

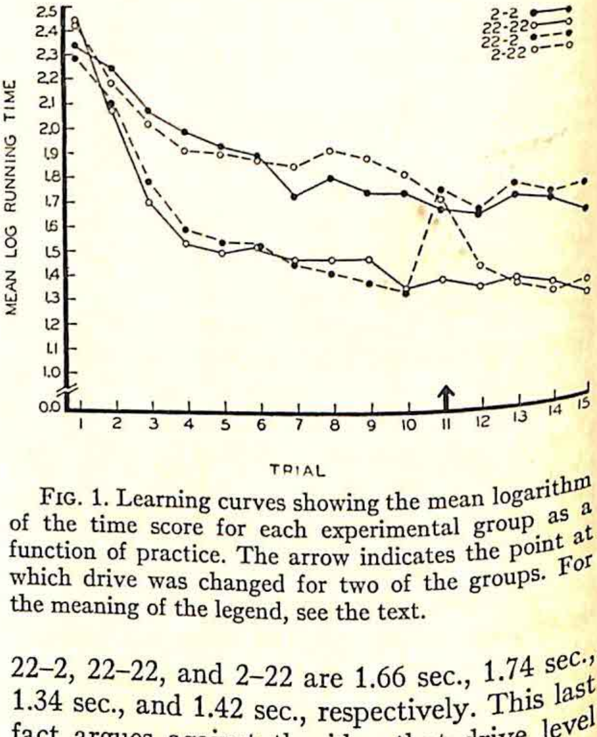

FIG. 1. Learning curves showing the mean logarithm of the time score for each experimental group as a function of practice. The arrow indicates the point at which drive was changed for two of the groups. For the meaning of the legend, see the text.

DISCUSSION

The results of this experiment are similar to those of Kendler (6), Strassburger (10), and Teel (11) in showing that drive level at the time of learning has no significant effect on behavior in a test situation when drive is equated. So far as the main question under investigation is concerned, they support Hull's (5) guess that motivation is important in response evocation but not in habit formation.

At another level, however, these findings are potentially damaging to one of Hull's fundamental assumptions, that various response measures depend for their value upon a single terminal construct, ${}_s\bar{E}_R$. From our results it appears, as Anderson (1) and Bruce (2) have previously found, that measures involving a time dimension are more responsive to motivational changes than measures like number of errors, which are independent of time. Such a result indicates that these two indices of response strength may be reflecting quite different aspects of behavior. In this respect the situation is like that in conditioning where low correlations between response latency and probability of occurrence are typically found (3). Although the response-evocation process described by Hull can accommodate such low correlations, results like those of the present experiment suggest at least a reconsideration of the widely accepted notion that all response variables depend equally upon a single process.

SUMMARY

Four groups of ten male albino rats were given 15 trials in a ten-unit T maze in an experiment designed to determine whether motivation at the time of learning influences the amount learned. Two groups received all their trials under 2 and 22 hr. of water deprivation, respectively. The other two groups received ten trials under these two conditions and then were shifted to the other condition. Analysis of maze performance in the last five trials shows no effect of earlier motivation on either time or error scores. Motivation *at the time of testing*, however, does influence time scores ($p = .001$). This fact supports Hull's hypothesis that the habit-formation process is independent of drive. The finding that time and errors respond differently to motivational changes suggests a re-examination of the relationship postulated by Hull to exist among the response variables.

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SIMPLE TRIAL-AND-ERROR LEARNING: MASSED AND DISTRIBUTED TRIALS WITH HABITS OF UNEQUAL INITIAL STRENGTH

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Hull (1) has investigated animal learning under conditions which he refers to as "simple trial-and-error learning." The term denotes a situation in which *E* first establishes in his *S*s two specific response habits with a given number of reinforcements for each response. Following this habit training he allowed the *S*s to make either response, but only one of the responses was reinforced. This second phase of training constituted the simple trial-and-error learning situation. Hull's experiment involved responses which had received unequal numbers of reinforcements in preliminary training. The *S*s were given massed trial-and-error learning trials. The present experiment is similar in plan to Hull's, except that in addition to a group of *S*s which received massed trial-and-error learning trials there was a comparable group for which the trial-and-error learning trials were distributed at the rate of approximately one trial per day.

METHOD

Subjects and Apparatus

The *S*s for the experiment were 90 male albino rats obtained from the Albino Farms, Redbank, New Jersey. All animals were 80 to 100 days old at the time of shipment.

The experimental box used was a modification of the Skinner-Youtz apparatus similar to that used by Hull (1) but with some modifications. The manipulanda entered the experimental chamber through two openings on either side of the food delivery chute. The manipulandum on the left (H-tube) was a piece of hollow brass tubing which could be moved horizontally. The manipulandum on the right (V-bar) was a piece of flat brass stock which could be moved vertically. The manipulanda were automatically retracted after a ¼-in. displacement in either direction from their positions of rest.

Further modifications included an open-ended hall, 5 in. high by 5¾ in. wide, which was placed inside the experimental chamber to restrict the activities of the *S*s. A vertically moving sheet-metal shutter 1 in. from the end of the hall allowed *E* to control the *S*s' access to the manipulanda. Water was provided by a bottle recessed in the door of the chamber at the end opposite from the shutter and manipulanda. Food pellets were delivered to the chute by hand.

Procedure

Habituation

All animals were allowed at least one week in which to recover from the effects of shipment. During this period a 24-hr. feeding cycle was begun, the animals being fed once a day at the time they were later to be trained. The day before being placed in the apparatus for the first time all animals were fed the food pellets used as reward in place of their regular food.

On the first day the animals were placed in the apparatus, they were allowed to explore it and to eat food pellets placed in the food cup. After the pellets in the food cup were eaten, an additional pellet was delivered through the food chute, accompanied by the sound of the electrical contact mechanism. Each animal remained in the apparatus until a total of 20 pellets had been obtained and eaten immediately following delivery. On the second day the animals received 20 additional pellets in the same way, except that this time the shutter in front of the food cup was raised before the delivery of each pellet and lowered after the animal had received the pellet. Any animal which was not finding and eating the pellets immediately on delivery was fed 20 additional pellets in the apparatus.

Habit Training

First session. After the animals had received five pellets accompanied by the click of the mechanism and by the raising and lowering of the shutter,[2] the shutter was lowered and a single manipulandum (smeared with wet food on the first three trials) was pushed into the animal's side of the apparatus. For one-half of the animals this manipulandum was the H-tube, and for the other half it was the V-bar. The shutter was then raised and the animal allowed to react until the manipulandum was displaced enough to cause it to be retracted. Food was given immediately following the retraction, and the shutter was lowered as soon as the animal had obtained the reward pellet.

The second trial was given as soon as the animal had finished eating and had returned to the vicinity of the food dish. The interval between trials was usually about 25 sec., although on occasions it was considerably longer, as when the animal drank after eating or indulged in random or exploratory activity.

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[1] This experiment is part of a dissertation presented to the faculty of Yale University in partial fulfillment of the requirements for the Ph.D. degree. The writer is indebted to the late Dr. Clark L. Hull, who served as thesis adviser and whose theoretical formulations provided the basis for the research. He also wishes to express his appreciation to Connecticut College for Women, which provided research facilities and funds for the experiment.

[2] This "warming-up" procedure was followed in each of the four sessions of habit training.

A total of 20 trials following this procedure constituted the first habit-training session. The response reinforced in this session was the response which was to be "*strong*" (have the greater habit strength) prior to trial-and-error learning, but which would be "*false*" (nonreinforced) in the trial-and-error learning. It will be referred to hereafter as $R_{s\text{-}f}$.

Second session. One week after the first habit-training session the animals were placed in the apparatus and the alternative manipulandum was introduced singly to the experimental chamber. Ten rewarded responses, following the procedure of the first session, established the habit strength of the response which would be "*weak*" prior to trial-and-error learning, but which would be "*correct*" (reinforced) in that situation. This response will be referred to as $R_{w\text{-}c}$.

Third session. Three days following the second session the animals were given 20 additional rewarded responses, the manipulandum for $R_{s\text{-}f}$ being presented singly.

Fourth session. Three days following the third session the animals were given 5 additional rewarded responses, the manipulandum for $R_{s\text{-}f}$ being presented singly.

At the end of the habit-training sessions each animal had received 45 reinforcements of $R_{s\text{-}f}$ and 10 reinforcements of $R_{w\text{-}c}$.

Trial-and-Error Learning

Group D, distributed trials. Following the fifth trial of the fourth habit-training session the shutter was lowered, both manipulanda were introduced to the experimental chamber, and the shutter was then raised. If the animal made the $R_{s\text{-}f}$ response, both manipulanda were retracted and the shutter was lowered. No reward was given for $R_{s\text{-}f}$. If the animal made the $R_{w\text{-}c}$ response, both manipulanda were automatically retracted, but a food pellet was delivered before the shutter was lowered. In trial-and-error learning $R_{w\text{-}c}$ was followed by food reward.

When an animal failed to make either response within 5 min. following the raising of the shutter, this was counted as a trial, and the animal was returned to its cage.

Group D animals received 100 distributed trial-and-error learning trials with a minimum interval of 24 hr. between trials. On 13 occasions the interval was 48 hr., and on one occasion the interval was 72 hr. All animals had been deprived of food in their cages for a period of 22 hr. prior to each trial.

Group M, massed trials. The animals of Group M were treated the same as animals in Group D, except that these animals were given 100 consecutive trials in the trial-and-error learning situation. The term "consecutive" as used here implies not only that the 100 trials were given in a single block but also that one trial followed another as soon as the animal had eaten the reward pellet and returned to the vicinity of the food cup. When no reward was given, the next trial was begun as soon as the manipulanda could be reset and the shutter raised if the animal remained in the vicinity of the food cup.

Two animals, on one occasion each, showed no tendency to react to either manipulandum within a 5-min. period following the raising of the shutter. On the following day the remainder of the 100 massed trials was given to each animal.

RESULTS

Before the results for Group D and Group M animals can be compared, it is necessary to establish the equivalence of the groups at the outset of trial-and-error learning. A convenient criterion is the distribution of $R_{s\text{-}f}$ and and $R_{w\text{-}c}$ responses for the two groups on the first trial-and-error learning trial. Group D gave 38 $R_{s\text{-}f}$ and 7 $R_{w\text{-}c}$ responses on this trial, and Group M gave 39 $R_{s\text{-}f}$ and 6 $R_{w\text{-}c}$ responses. The chi-square value for the distribution of responses obtained is .09, which has a probability of between .70 and .80 of being exceeded in random samples drawn from the same universe of subjects.

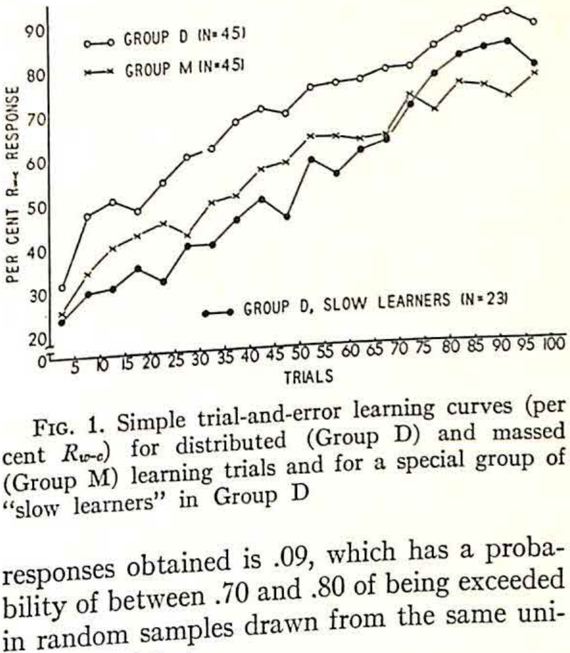

FIG. 1. Simple trial-and-error learning curves (per cent $R_{w\text{-}c}$) for distributed (Group D) and massed (Group M) learning trials and for a special group of "slow learners" in Group D

Rate of Learning $R_{w\text{-}c}$

These data are presented in Figure 1 where rate of learning $R_{w\text{-}c}$ is presented in terms of the percentage of *S*s making the $R_{w\text{-}c}$ (reinforced) response. The first point for each curve represents the mean percentage of $R_{w\text{-}c}$ in the first five trials, the second point the mean for the next five trials, etc. "Group D, slow learners" were the 23 *S*s in Group D which gave the fewest $R_{w\text{-}c}$ responses in the 100 trial-and-error learning trials.

The data presented in Figure 1 should be considered (and will be discussed) from two points of view: first, the relative rates of learning the R_{w-c} response when the learning trials are massed and when they are distributed; second, the general shape of the learning curve.

Number of Alternation Cycles

An alternation cycle is defined as two consecutive response phases. One response of a particular kind, either R_{s-f} or R_{w-c}, or more than one consecutive response of the same kind constitutes a response phase. For Group D the mean number of alternation cycles for 45 *S*s was 10.0 (*SD* 4.0). For Group M the mean number of alternation cycles for 45 *S*s was 15.2 (*SD* 5.1). The value of *t* for the difference between the means was 5.2. The value of *t* required for a difference to be considered statistically significant at the .01 level of confidence is 2.6.

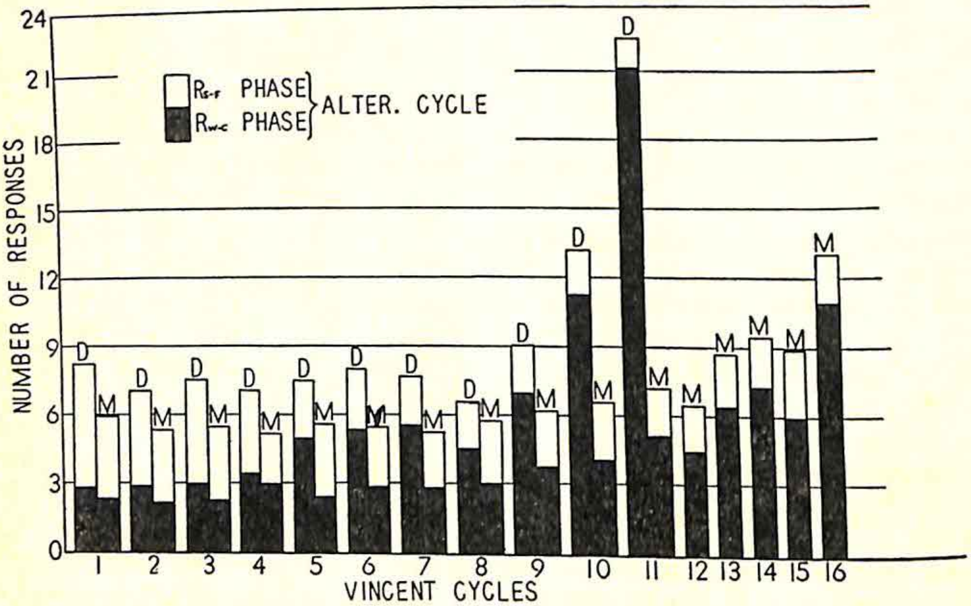

FIG. 2. Mean number of responses per R_{s-f} and R_{w-c} response phase and per alternation cycle for distributed trials learning (D) and massed trials learning (M) subjects

Relative Length of R_{s-f} *and* R_{w-c} *Response Phases*

The length of R_{s-f} and R_{w-c} response phases as a function of the number of alternation cycles is shown in Figure 2. Response phases and alternation cycles for Group D are based on the records of 38 *S*s (out of 45 in this group) which completed 6 or more alternation cycles, including the cycle which was terminated by the end of the learning trials. The mean number of cycles given by these *S*s was 11.3. The values for each alternation cycle and response phase are the mean values for these *S*s, whose responses have been divided proportionately into 11 cycles. The corresponding data for Group M were derived from the records of 42 *S*s which completed 7 or more cycles. The mean number of alternation cycles for the *S*s included was 16.0, so each record was divided into 16 proportional parts.

The length of alternation cycles as a function of the number of cycles is also shown in Figure 2.

DISCUSSION

The primary purpose of the present experiment was to test certain hypotheses based upon Hull's *Principles of Behavior* (2) and formalized in the manuscript "Elementary Theory of Individual Behavior" (3).

One hypothesis was that at any given point in the trial-and-error learning process short of complete mastery the *S*s learning in distributed trials would show a higher percentage of correct responses than would the *S*s learning in massed trials. The principal theoretical consideration leading to this conclusion is that in the case of massed learning trials there is a cumulative drive reduction as learning proceeds. The motivation involved is, presumably, hunger, for the animals had not been fed for 22 hr. prior to training. For each correct response ($R_{w\text{-}c}$) in trial-and-error learning the Group M animals got a food reward. This is assumed to reduce drive, so that even though subsequent reward pellets are objectively equal in weight, they produce progressively smaller increments in habit strength. For Group D animals, however, each pellet breaks an involuntary fast of 22-hr. duration. It is assumed that for animals in this group each reward pellet after the first produces a relatively greater increment in habit strength than it does for Group M animals, hence faster learning of the correct response for Group D.

Figure 1 illustrates the agreement of the data from this experiment with the experimental hypothesis. Although on the first trial-and-error learning trial there is no significant difference in percentage of $R_{w\text{-}c}$ responses between Group D and Group M *S*s, the mean of the first five learning trials shows a definite superiority for Group D in percentage of $R_{w\text{-}c}$ responses. The graph shows the continuity of this superiority for Group D, which superiority begins to diminish only as both groups approach a level of approximately 90 per cent $R_{w\text{-}c}$ responses.

A second hypothesis was that the number of alternation cycles would be greater for the group of *S*s receiving massed trial-and-error learning trials than for the group receiving distributed trials. The crucial assumption in the derivation of this hypothesis is that in the case of massed learning trials reactive inhibition, I_R (2), summates with conditioned inhibition, ${}_sI_R$, to end any particular response phase. In distributed trials reactive inhibition is of little or no importance; consequently, *S*s can be expected to perseverate longer on a particular type of response. This increases the length of response phases and alternation cycles and produces fewer alternation cycles in a given number of trials for the distributed learning trials group. The results obtained in the present experiment support this hypothesis insofar as the difference in the number of alternation cycles for Group M and Group D animals cannot be attributed to chance variations in behavior for samples chosen from the same universe of animals.

The remaining hypotheses had to do with aspects of simple trial-and-error learning without special regard to the spacing of trials as a variable. On theoretical grounds it was expected that the $R_{s\text{-}f}$ response phase would be longer initially than the $R_{w\text{-}c}$ response phase but would gradually become shorter than the $R_{w\text{-}c}$ response phase as learning progressed. In this learning situation the effective reaction potential, ${}_s\bar{E}_R$ (2), for the incorrect response is progressively decreased through nonreinforcement, and the effective reaction potential for the correct response is increased by reinforcement. The occurrence of one response or the other on a given trial is determined by the oscillation, ${}_sO_R$, of momentary effective reaction potential for each response. So long as the effective reaction potential for $R_{s\text{-}f}$ is greater than the reaction potential for $R_{w\text{-}c}$, probability favors a series of $R_{s\text{-}f}$ responses. As soon as the effective reaction potential for $R_{w\text{-}c}$ becomes greater, probability favors a series of $R_{w\text{-}c}$ responses. Figure 2 illustrates the substantiation of the experimental hypothesis for both Groups M and D.

A simple extension of the above reasoning explains the next hypothesis, namely, that when length of alternation cycle is plotted against number of cycles, the resulting curve should be U shaped. As the effective reaction potentials for $R_{s\text{-}f}$ and $R_{w\text{-}c}$ approach equality, the probability of evoking either response on a given trial approaches .50. It is then unlikely that one will obtain a long series of either $R_{s\text{-}f}$ or $R_{w\text{-}c}$ responses. By definition it follows that if response phases are short, alternation cycles must be short also. The relative height of the left half of the U-shaped curve is dependent on the difference in habit strength for $R_{s\text{-}f}$ and $R_{w\text{-}c}$ at the outset of trial-and-error learning. When there is no difference, the curve is expected to show positive acceleration from the beginning.

The present experiment does not afford a clear-cut basis for evaluating the experimental hypothesis, although it may be stated that every alternation cycle until the ninth for each group was shorter than the initial cycle. The progressive lengthening of the alternation cycles in the latter stages is apparent in Figure 2. However, the existence of a definite left arm of the U-shaped curve is not obvious. In line with the reasoning of the preceding paragraph, this can be attributed to a failure to produce sufficient difference in the habit strengths for $R_{s\text{-}f}$ and $R_{w\text{-}c}$ in preliminary training.

The final hypothesis refers to the shape of the simple trial-and-error learning curve when per cent $R_{w\text{-}c}$ is plotted against number of learning trials (Fig. 1). So long as the effective reaction potential for $R_{s\text{-}f}$ is greater than that for $R_{w\text{-}c}$, the learning curve should be positively accelerated (3). At the point where the effective reaction potentials for the two responses are equal (indicated empirically by 50 per cent $R_{w\text{-}c}$ response), the learning curve should shift to one of negative acceleration. For Groups D and M not enough of the learning curve below 50 per cent $R_{w\text{-}c}$ response was obtained in this experiment to permit an evaluation of this part of the learning curve. Even the 23 slowest learners in Group D, whose learning curve is plotted separately in Figure 1, provide inadequate evidence for evaluating the hypothesis. Both this slow-learning group and Group D as a whole show the negative acceleration expected when the per cent $R_{w\text{-}c}$ is greater than 50. Data for Group M, however, appear ambiguous to the writer even on this part of the hypothesis.

SUMMARY

Ninety albino rats were given 45 food reinforcements for response $R_{s\text{-}f}$ and 10 food reinforcements for response $R_{w\text{-}c}$ in a modified Skinner-Youtz apparatus. Following this the *S*s were permitted to make either response, but only $R_{w\text{-}c}$ was followed by food reward. These constituted the "simple trial-and-error learning" trials. For half the *S*s the choices between $R_{s\text{-}f}$ and $R_{w\text{-}c}$ were distributed at the rate of one trial per day. For the other half of the *S*s the 100 trials occurred in a single experimental session.

The results obtained indicate that:

1. The correct response ($R_{w\text{-}c}$) is learned more rapidly in distributed trials than in massed trials.

2. The number of shifts from one type of response to the other is significantly greater for massed than for distributed learning trials.

3. Persistence in consecutive $R_{s\text{-}f}$ responses is at first greater than, but becomes less than, persistence in consecutive $R_{w\text{-}c}$ responses under both conditions of learning.

4. Alternation cycles (two series of consecutive responses) may either decrease or remain relatively constant in length in the early stages of learning, but definitely increase in length in the latter stages.

The data obtained did not permit evaluation of the experimental hypothesis that the learning curve for the correct response would be sigmoid with a positive initial acceleration.

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DISCRIMINATION LEARNING BY RHESUS MONKEYS TO VISUAL-EXPLORATION MOTIVATION[1]

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Experiments conducted at the University of Wisconsin Primate Laboratory have demonstrated that rhesus monkeys learn the solution of mechanical puzzles to no other incentive than that provided by the manipulation of the puzzle devices (4, 1, 2) and that these manipulatory responses will persist during prolonged repetitive testing (3). Recently, monkeys have been trained without food or other special incentives to discriminate between differentially colored sets of screw eyes (5). A manipulation drive has been postulated as the motivational basis for this type of behavior, and Harlow postulates that manipulation drive is "one of a class of externally elicited drives" (3, p. 293).

The present experiments were designed to test the efficacy of another kind of externally elicited motive, that of visual exploration. Monkeys both in their home cages and in test situations continually follow movements of objects and people in their field of vision and persistently explore their environment visually.

Two preliminary experiments were conducted to investigate visually motivated behavior. Experiment I, designed primarily to measure learning, involved testing three monkeys 20 trials a day (an hour or less) for 20 days on a color discrimination, with no other incentive provided than visual exploration. Experiment II, designed primarily to test strength and persistence of visual motivation, involved testing two monkeys 4 hr. a day for 5 days under visual-exploration incentive.

METHOD

Subjects

Three rhesus monkeys, no. 156, 159, and 167, served as *S*s in Experiment I, and two rhesus monkeys, no. 102 and 147, served as *S*s in Experiment II. All animals were adult and had had very extensive previous training on food-rewarded learning problems. Numbers 156, 159, 102, and 147 had been *S*s in manipulation-drive studies.

Apparatus

During testing the monkeys were housed in a wire cage 27 by 17 by 26 in. Over this cage *E* placed a box with front and top made of pressed wood and three sides covered by heavy black cloth. A 25-w. lamp was fastened on the roof of the box to provide illumination within. Two doors measuring 3¾ by 4 in. were fastened, flush, to the front of the box, with their bases 12 in. above the floor and 5 in. apart, center to center. Each door could be locked by a wooden pin, and each locking device contained a leaf switch connected to a 6-v. battery. When the door was pushed, contact was made with the locking device and an electric circuit was completed, illuminating a small signal light mounted on the front of the apparatus. Transparent Lucite plates 3 in. by 3 in. were mounted on the inside face of each door so as to permit differentially colored stimulus cards to be inserted between the Lucite plate and the door. An opaque screen, which could be raised or lowered by *E*, separated *S* from the stimulus cards. The apparatus stood on a table in the entrance room of the Wisconsin primate laboratory. The temperature in the test room ranged from 70° to 80°F. The temperature within the test box increased 6° to 7°F. above room temperature during the 4-hr. test sessions.

Procedure

Preliminary training. During preliminary training both doors, with neither holding a stimulus card, were closed, and one of the doors was always left unlocked, the position of the unlocked door on successive trials being determined by a sequence balanced for positional frequency. The *E* initiated each trial by raising the opaque screen and exposing the doors to the animal. If the monkey pushed against and opened the unlocked door, it was permitted 30 sec. to view the surroundings. The *E* then lowered the screen, ending the trial. If it pushed against the locked door, *S* was allowed 5 min. to try the other door. At the end of this time the door was opened by *E* for 30 sec., the screen then lowered, and the trial concluded. The intertrial period was always 30 sec. Preliminary training consisted of 20 trials a day for two days.

Discrimination training. In Experiment I the *S*s were tested on a yellow-blue discrimination, blue being the positive stimulus for monkeys 159 and 167, and yellow the positive stimulus for monkey 156. The position of the positive and negative cards followed a predetermined balanced order.

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[1] These researches were supported in part by a grant to the University of Wisconsin from the Atomic Energy Commission Contract No. AT(11-1)-64 and in part by the Research Committee of the Graduate School from funds supplied by the Wisconsin Alumni Research Foundation.

The animals were placed in the apparatus for 5 min. each day before testing began. The *E* initiated each trial by raising the opaque screen, exposing the stimulus cards. If *S* pushed open the door containing the positive stimulus, it was allowed 30 sec. of visual exploration before the screen was lowered. If *S* pushed against the door with the negative card, the door engaged the locking device, illuminating the signal light, and the screen was immediately lowered. The intertrial interval was always 30 sec., during which the stimulus cards were either rearranged or removed and returned to their previous position. A noncorrection technique was used throughout. Each animal received 20 trials a day, 5 days a week, for a total of 20 days. The time of the day for testing was not held constant. The response measures recorded were errors and response latencies, defined as time between *E*'s raising the screen and *S*'s responding to a door. The testing procedures for Experiment II were the same as those described for Experiment I except that the *S*s were tested continuously 4 hr. a day for five days with a day's rest between days 3 and 4 only. The blue card was positive for monkey 102 and the yellow card positive for monkey 147.

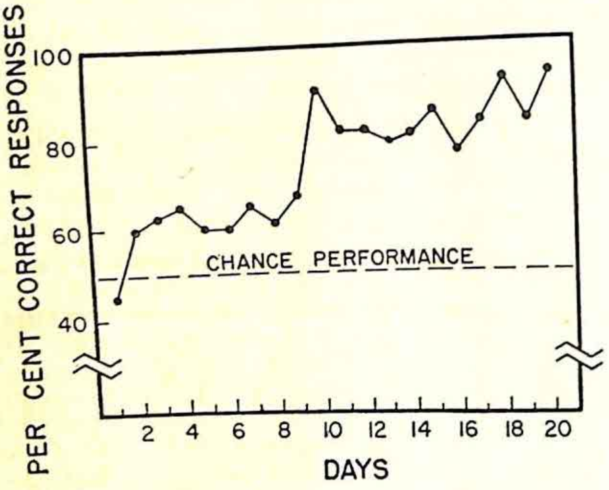

FIG. 1. Discrimination learning to visual-exploration incentives

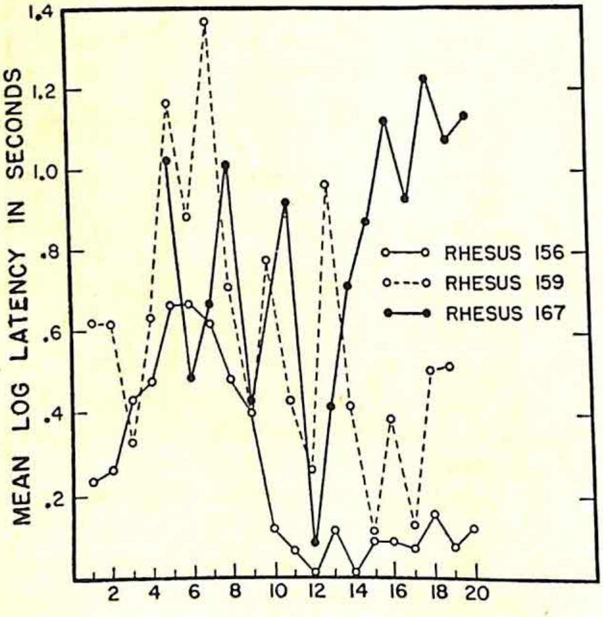

FIG. 2. Response latencies to visual-exploration incentives

During both experiments people were frequently in the test room for a part of each session. When *S* opened the door, *E*, after recording the data for the trial, usually walked around the room, opened cabinets, or stepped outside the building within the 30-sec. period. Thus, the animals ordinarily were provided with a diversified environment in which several activities occurred and which offered auditory as well as visual stimulation. Care was taken to prevent the monkeys from seeing either food or other monkeys during the test sessions.

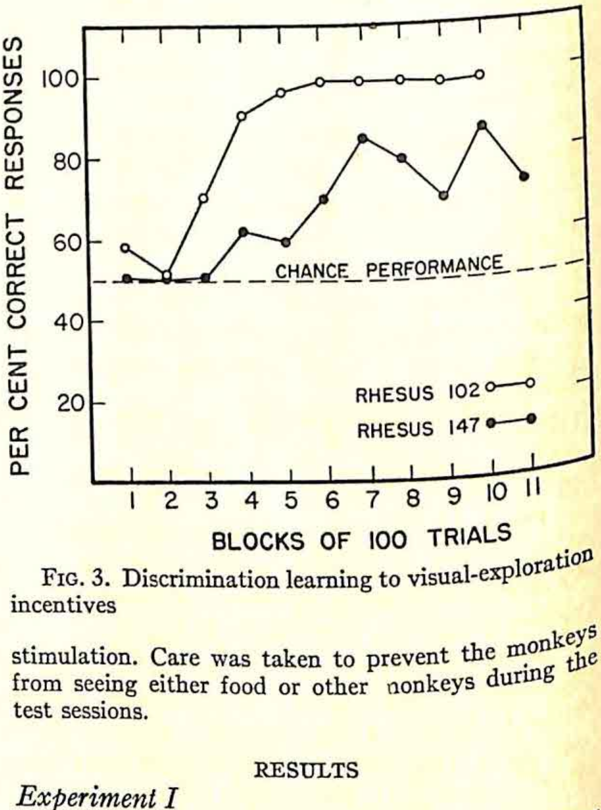

FIG. 3. Discrimination learning to visual-exploration incentives

RESULTS

Experiment I

The mean percentage of correct responses made by the three monkeys is shown in Figure 1 and clearly demonstrates learning. Animals 156, 159, and 167 attained 17 correct responses in 20 trials (performance significantly better than chance at the .01 confidence level) on days 7, 10, and 12, respectively, and they equaled or exceeded this level on 11, 7, and 2 succeeding days, respectively.

Figure 2 shows the mean log response latencies made by the three monkeys on the 20 test days. Response latencies for animal 156 increase during learning and then drop to, and are maintained at, a low level. Similar results except for greater interday variability are obtained for animal 159. Response latencies for animal 167 increase during the second half of the experiment.

Experiment II

The individual discrimination-learning curves for the two *S*s of the second experiment are plotted in Figure 3. Number 102 attains and then maintains almost perfect performance; no. 147 performs consistently during the last 600 trials at a level significantly better than chance at the .01 confidence level.

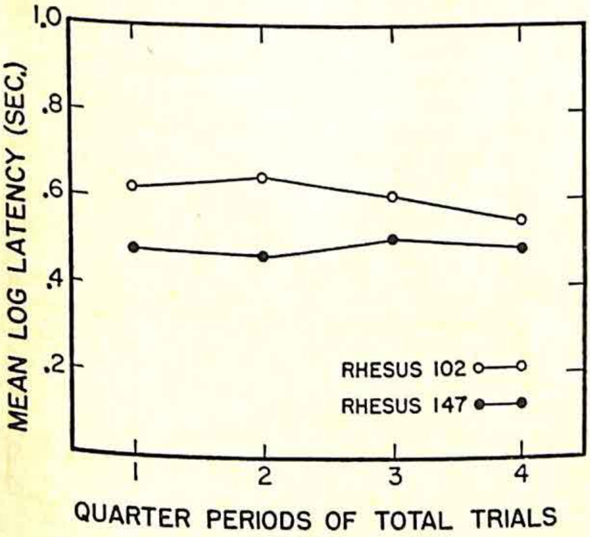

Fig. 4. Response latencies within test periods

Figure 4 shows the mean log response latencies within test periods. The total trials made by each animal each day were divided into fourths of total daily trials and then averaged for all five days. These data show that the animals responded at a relatively constant and rapid rate throughout the 4-hr. test sessions. The data of Figure 5 give no indication of increasing response latencies during the course of the five days of testing. The response latencies for monkey 147 actually are at their lowest on days 4 and 5.

Additional Performance Measures

Although records of vocalization and cage-shaking had not been planned and were not systematically made, the *E*s were impressed by the extreme paucity of vocalizations. The monkeys appeared to be quieter in the test situation than in their home cages or standard laboratory test rooms. Only monkeys 147 and 167 shook their cages, 167 infrequently, 147 more often. Cage-shaking was certainly no more frequent than in the home situation. Monkey 147 was a mature and unusually large, violent, aggressive male.

Defecation was not frequent in any animal except no. 159, and amount of defecation, commonly and appropriately accepted as a measure of emotionality in monkeys, tended to decrease during the course of the experiment

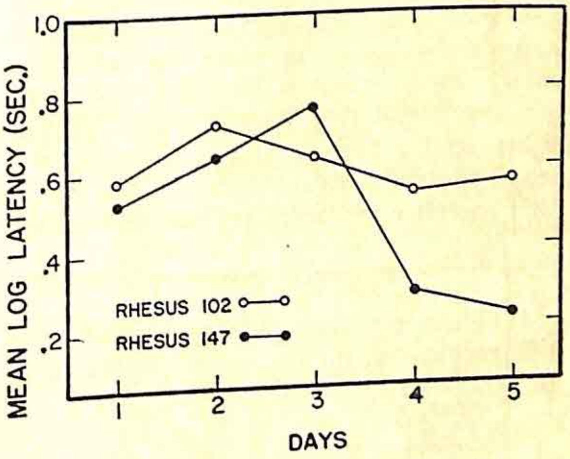

Fig. 5. Response latencies as a function of days

DISCUSSION

These experiments demonstrate beyond question that monkeys can learn object discriminations and maintain their performance at a high level of efficiency with visual-exploration reward.

The persistence of visual-exploratory motives throughout long daily test sessions and throughout series of daily test sessions also testifies to the importance, strength, and persistence of these motives elicited by external stimuli. Monkeys 156 and 159 show little or no decrease in motivational strength as indicated by response latency measures throughout 20 days of testing in Experiment I (see Fig. 2). Similarly, monkeys 102 and 147 show no decrease in motivational strength either during test days (see Fig. 4) or on successive test days (see Fig. 5) in Experiment II.

The efficient maintenance of visual-explora-

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tion motivational strength in these animals argues strongly against any explanation in terms of secondary reinforcement, for second-order conditioned responses not based on unconditioned pain responses tend to extinguish rapidly. The lack of evidence of disturbed behavior—either somatic responses of vocalization or violence, or visceral responses of defecation—would appear to render any explanation of this behavior in terms of anxiety improbable unless one wishes to define anxiety in terms of any and all conditions of deprivation.

The most obvious and acceptable explanation for the observed performances of the monkeys lies in the hypothesis that monkeys—and presumably all primates—have a strong motive toward visual exploration of their environment and that learning may be established on the basis of this motive just as it may be established on the basis of any motive that regularly and reliably elicits responses.

CONCLUSIONS

1. Five rhesus monkeys learned a discrimination problem on the basis of a visual-exploration incentive.

2. Efficient performance was maintained during the long daily sessions and throughout a series of daily sessions with little or no evidence of satiation.

3. A visual-exploration motive is hypothesized on the basis of the obtained data, and it is suggested that this motive is strong, persistent, and not derived from, or conditioned upon, other motivational or drive states.

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DISCRIMINATION LEARNING SET IN CHIMPANZEES[1]

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The study of learning sets, as introduced by Harlow (1, 2), appears to offer new possibilities for the investigation of comparative intelligence, especially among the higher primates, where tests can be used in essentially the same form without overtaxing the sensory or motor capacities of any species. Although this report will give a rough indication of the chimpanzee's position on the learning-set scale, it will not be definitive. Precise comparison of man, ape, and monkey must await a more adequate understanding of learning sets. For instance, we must know more about the relative efficiency of various training methods, and the relationship of set development to age and pre-experimental experience. The present investigation has been concerned with problems of this type, as well as with approaching an eventual species comparison.

METHOD

Subjects

Eight chimpanzees, ranging in age from 15 months to 26 years, were used in this work. None of them had prior experience with more than a few visual-discrimination problems. One, Viki, had spent her life in a human home. Six human children, from 2 to 7 years of age, were also used. Individual ages of all *S*s will be given in connection with the results.

General Procedure

Our methods have been much like those described by Harlow, but have differed in several ways which may have influenced the results. Our chimpanzees worked in the outdoor sections of their regular living cages. They did not seem to be seriously distracted by extraneous stimuli in this familiar environment. The cages are made of coarse wire mesh, through which the *S*s reached to displace the test objects and take the rewards.

The test apparatus was mounted on wheels, for convenience in moving from cage to cage. It contained a horizontally sliding tray with two food wells, and a vertically sliding opaque screen, which was lowered to conceal the tray between trials. There was no one-way vision screen, but the opaque screen was normally raised so slightly that the subject could see very little of *E* while making a choice.

To increase the probability that *S* would look at both objects before displacing one, the tray was held in the half-forward position for several seconds at the beginning of each trial. It was then advanced to within *S*'s reach.

On the assumption that it might facilitate insight into the nature of the problems, and minimize errors due to exploratory tendencies, our *S*s were allowed to displace both objects, successively, on each trial. When the initial choice was incorrect, a delay of approximately 5 sec. was imposed before correction, by withdrawing the tray just out of reach. (When the first choice was correct, the remaining object was seldom displaced, except early in training.)

Appropriate modifications of this procedure were used with the human children and the home-raised chimpanzee, Viki.

About 600 test objects were available. Most of them were made up of various combinations of wood, metal, plastic, cloth, paper, and assorted hardware, often with colored lacquer added. They were arranged in pairs by selection of two objects differing markedly in several visual characteristics. One of the pair was designated correct by the toss of a coin, and the pairs were arranged in series at random. Toward the end of the experiment, if additional pairs were needed, previously used objects were grouped in new pairs and re-used.

The early and late phases of training differed with respect to details of procedure and handling of data, and will be discussed separately.

EARLY PART OF SET DEVELOPMENT

Procedure. We have tentatively assumed that learning set is a function of the number of problems learned, in which case a problem would be wasted if it were dropped before it was learned, and trials would be wasted if training were continued beyond mastery. With most of our *S*s, therefore, the early problems were run to a criterion—five successive correct choices if preceded by less than ten trials; ten successive correct if preceded by ten or more. Two chimpanzees, Vera and Hank, were started at fixed rates of two and ten trials per problem, respectively.

Results. Figure 1 shows the results of this training, for individual subjects. Except in Hank's case, progress is plotted in terms of errors after the first trial, as a function of the number of problems solved. This seems to us the most appropriate type of curve for the early stages of set training, where learning initial chance level. Figure 1 gives a more complete picture of this early development.)

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[1] This investigation has been assisted by grants from the American Philosophical Society and the Samuel S. Fels Fund.

MISCELLANEOUS RESULTS

Additional chimpanzees. Three of our *S*s are not included in the figures, and their results will be summarized briefly. Don (17 yr.) received extensive early training which was too unsystematic to be analyzed. His later training consisted of 250 problems for two trials each, during which his second-trial accuracy remained around 90 per cent.

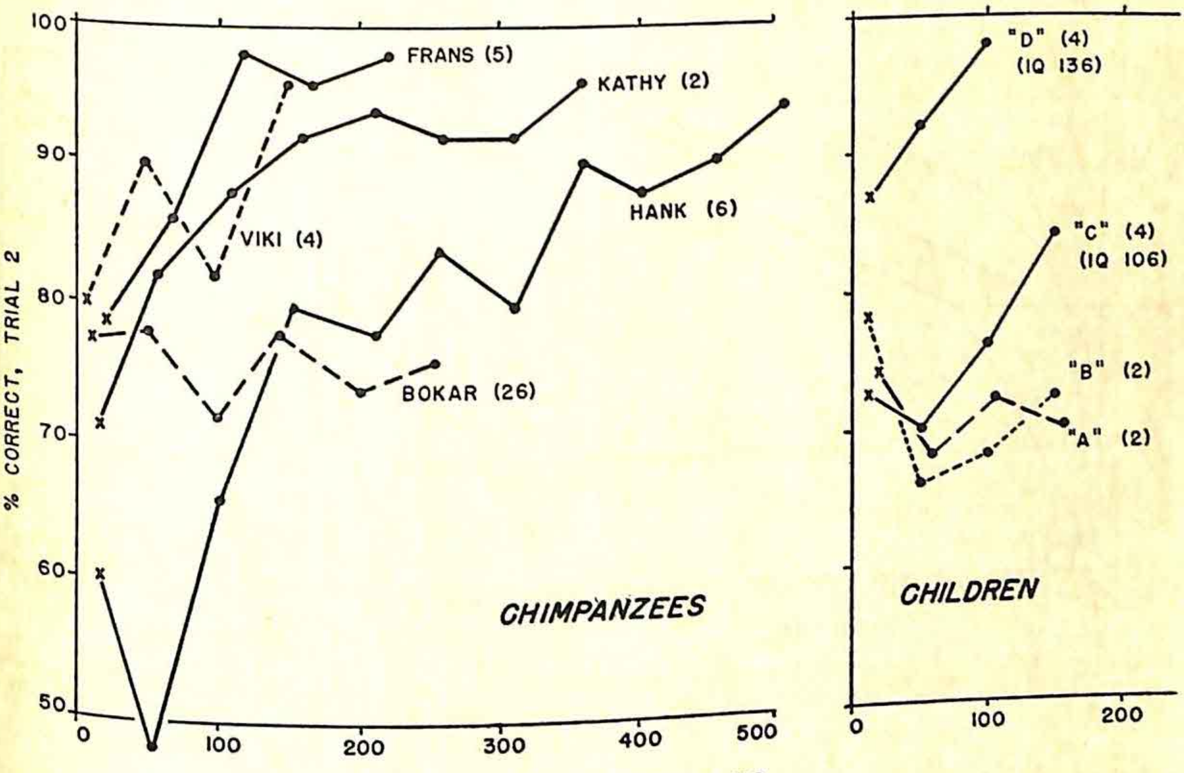

FIG. 2. The later phase of learning-set development. *X* indicates points based on the first 15 to 42 problems, which were run for a number of trials. Circles are points based on 50 problems, each run for two trials.

Vera (20 yr.) began training at a fixed rate of two trials per problem. Her second-trial accuracy remained at about chance level for 300 problems. She was then shifted to ten trials per problem, and began to improve rapidly.

To explore the lower age limit at which chimpanzees might be used in this work, we tried to train Neal from the age of 15 months to 17 months. We finally abandoned the effort—not because he could not learn, but because he did not work at it. Like most chimpanzees of this age, he had little interest in solid food; and since he liked to play with the test objects (baited as well as unbaited) it was difficult to score his performance in a meaningful way.

Verbal reports. Our human *S*s often discussed the work as it proceeded, and their remarks provide some clues as to what they had learned at various stages. Their comments referred to objects, rather than positions, almost from the beginning of training. This is in line with the fact that they solved occasional problems without errors, long before they did so consistently. (Such early, immediate solutions are also common in the chimpanzee data of Fig. 1.) The fact that the reward was always under the same object was mentioned by three of the children during the early phase of their training.

Their "object hypotheses" often lacked an objective basis, however. "C" (4 yr., IQ 106) usually announced her decision before making a choice on the first trial of a problem. If her choice proved incorrect, she often blamed the experimenter, chose the same object on the usually takes a number of trials. Since Hank was not trained to criterion, his performance is plotted in terms of errors on trials 2 through 10 of each problem, as a function of the number of problems presented.

For purpose of comparison, a typical one of Harlow's monkeys (No. 102) is also included in Figure 1. In this case, all 32 problems were originally run for 50 trials each, but the data are presented here in terms of errors before criterion.

LATER PART OF SET DEVELOPMENT

Procedure. In the later stages of training, the great majority of the problems are learned within the first few trials, so that training to criterion would be superfluous. Harlow (2) used six trials per problem at this point, and he reports (3) that Braun used three, which reduced the total number of trials required. In the present case we have pushed this trend to the limit, by using only two trials per problem—one training trial and one test trial. Ten problems were usually presented at a session.

Results. Figure 2 shows the progress of those subjects whose training was continued on this schedule. Results are plotted in terms of percentage correct on the second trial, as a function of the number of problems presented. This type of curve seems quite appropriate to the later phases of set development, where a large proportion of learning occurs on the first trial. When the second trial is the only test trial, this presentation includes all the data.

The first point on each of these curves represents the early training, where each problem was run for a number of trials. (These first points do not necessarily indicate *initial* performance, since each of them is based on a series of problems, during which second-trial accuracy may have increased rapidly from an

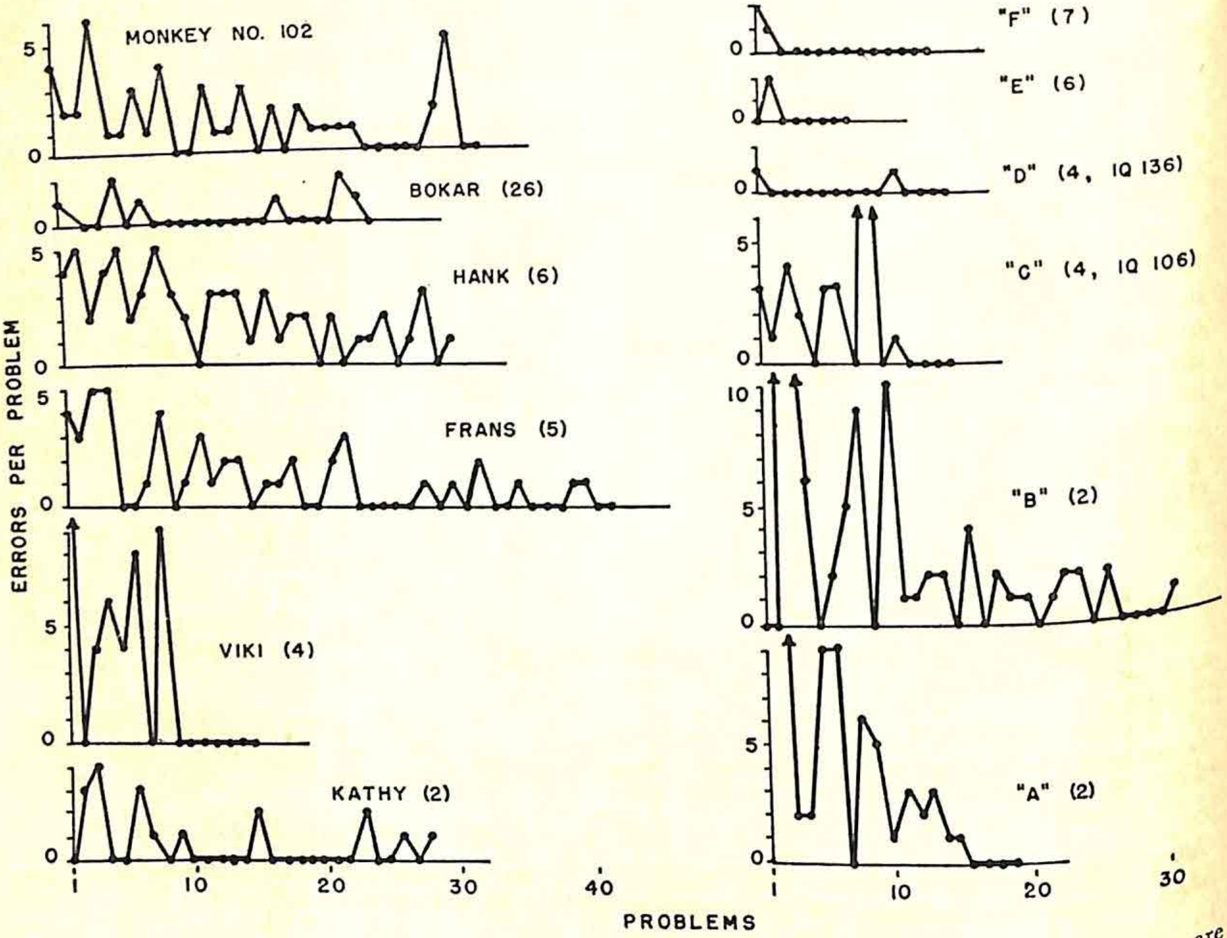

FIG. 1. The early phase of learning-set development. Human *S*s are designated by letters. Ages, in years, are given in parentheses, with IQ when available. We are indebted to Dr. Harlow for the use of his original data, from which the curve for monkey no. 102 was derived.

second trial, and scolded the experimenter again for continuing to bait the "wrong" object.

"D" (4 yr., IQ 136) also complained when her a priori hypothesis proved incorrect, but she readily altered the hypothesis to fit the facts. After about 80 problems, she suddenly remarked that the first trial was just a guess, and that it was only on the second trial that she could really know which object was correct. Her first choices were made slowly and carefully before this point, but much more quickly afterward.

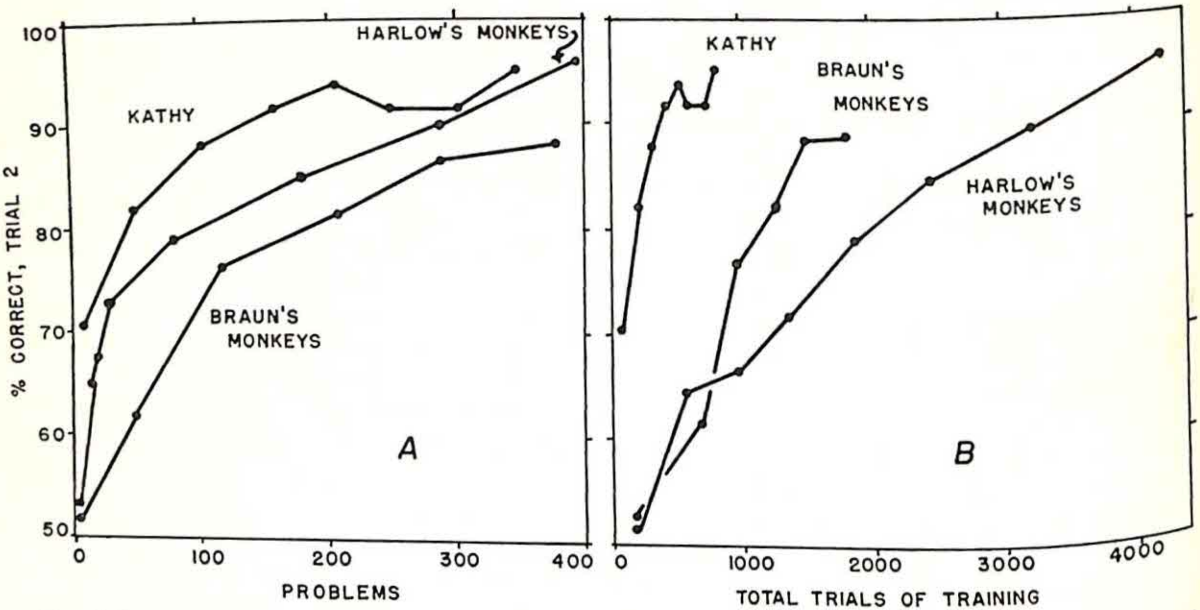

FIG. 3. Learning-set development as a function of problems (*A*) and trials (*B*). The curves for Harlow's and Braun's monkeys are based on data given by Harlow (3). Kathy's curve is included as representative of our chimpanzees.

"F" (7 yr.) stated this same principle on his eighth problem.

DISCUSSION

Stages of set acquisition. Although we have divided our presentation into early and late phases largely for convenience in exposition, the data suggest a more basic justification for this division. Figure 2 shows that our subjects made rapid progress until their second-trial accuracy was about 70 to 80 per cent, but that additional training produced much smaller gains per problem. The curves of Figure 3*A* show a similar change in slope. The existence of two different rates of progress suggests that two different learning processes may be involved. This suggestion is supported by a lack of correlation between the rates of early and late progress (compare Frans and Bokar in Fig. 1 and 2); and by the verbal reports of the human *S*s.

Venturing a crude and tentative interpretation, we would suggest that the early phase (during which learning time is quickly reduced to a few trials) may involve primarily the abstraction of general principles, such as: (*a*) One object is always baited. (*b*) One object is always unbaited. (*c*) The baited object may be in either position. (*d*) The same object continues to be baited throughout the problem.

The later phase (during which second-trial accuracy slowly increases beyond about 75 per cent) may involve primarily improvement in such skills or work habits as (*a*) looking carefully before choosing; (*b*) noting characteristics in which the two objects differ markedly; and (*c*) remembering what was learned on the first trial.

Early training methods. Our results with Hank and Vera suggest that early training with a small, constant number of trials per problem is quite inefficient. This is presumably due to the large proportion of problems which are dropped before they are learned. Harlow avoided this difficulty by running his early problems for a *large*, constant number of trials; practically all of his problems were mastered within the 50 trials allowed. This schedule gave a good gain per problem, as shown in Figure 3*A*; but it was quite inefficient in terms of total training trials, as shown in Figure 3*B*.

No fixed schedule of training can insure that each problem will be run long enough to be learned, but not long enough to be wasteful of trials. Training to criterion is the only way to run all problems long enough but no longer. To conserve trials, it is desirable to use the shortest criterial series that has a reasonable degree of statistical significance—which need not be high, since many problems are used, and no single one of them is of crucial importance.

Later training methods. The above considerations do not apply to the later stages of set development, where practically all problems are learned within the first few trials. A fixed number of trials per problem is appropriate at this point, and data are available for several such rates. Figure 3*A* shows that when second-trial accuracy is around 80 to 90 per cent, the gain per problem is much the same, whether problems are run for six trials (Harlow's monkeys), three trials (Braun's monkeys), or two trials (our chimpanzee, Kathy). The lower rates have the practical advantage of giving greater gains per trial, as shown in Figure 3*B*.

Age. Our chimpanzee data suggest that capacity to acquire a learning set does not increase with age, after the point where training becomes practical. Two-year-old Kathy did as well as 26-year-old Bokar on the early problems (Fig. 1) and much better on the later ones (Fig. 2).

The human children, however, appear to develop sets much more rapidly at later ages. Although this species difference could perhaps be ascribed to a difference in maturation patterns, we prefer to explain it in environmental terms: The human child's background of experience facilitates the development of informal learning sets which can readily be transferred to the experimental situation. We had hoped that the home-raised chimpanzee, Viki, would provide direct evidence on this point but, unfortunately, she was tested before the age at which human children may be depended on to display pre-experimental sets.

Language. Comparative psychologists frequently attribute the superior ability of human learners to their possession of language. In the present experiment, it might be assumed that human *S*s would derive advantage from being able to name the test objects—names presumably being easier to deal with than whatever "central representative processes" might otherwise be used.

Our human *S*s did, indeed, name many of the objects, but there was no indication that this helped them to learn either the individual problems, or the general principles of the experiment. "C," who was very talkative, often continued to make errors after naming the objects; but during one problem, which she solved very quickly, she reported: "I know it's right, but I don't know what it is."

The introspective reports of some of our colleagues, who have served as *S*s in more complicated object-discrimination problems, suggest that visual imagery may be more useful than language in such tasks, even for *S*s with a very high degree of language facility.

Species comparison. The data available suggest that when pre-experimental experience is equated, man, chimpanzee, and rhesus monkey differ very little in their ability to acquire sets for object-discrimination learning. It may well develop that the means of large groups will differ significantly, but it seems fairly certain that all three groups will overlap. On early training (Fig. 1), Harlow's monkey did about as well as our slowest human child, "B." On later training, the average curve for Harlow's six monkeys (Fig. 3*A*) indicates faster progress than the curves for three of our human children (Fig. 2).

SUMMARY

Five chimpanzees were given extensive training in visual-, object-discrimination learning. The course of their acquisition of learning sets is described. Results of supplementary work with three additional chimpanzees and six human children are also presented.

Analysis of the data from this and other studies leads to the suggestion that learning-set development may be meaningfully divided into qualitatively different early and late phases.

A learning set may be developed most efficiently by training to criterion on early prob-

lems, and by running later problems for a small, constant number of trials.

Age, per se, does not appear to be a factor in speed of set acquisition. Species comparisons should be made in terms of individuals with similar pre-experimental experience.

Man, chimpanzee, and monkey probably differ little in their abilities to acquire learning sets of this type.

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CONCURRENT DISCRIMINATION LEARNING IN CHIMPANZEES[1]

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One of the most unique characteristics of human behavior is the extent to which it utilizes large numbers of arbitrary associations concurrently, despite the possibilities of mutual interference among them. Language provides the most obvious example of this feature, but man's cultural way of life involves much more general use of a large "information-handling capacity." This aspect of behavior has received little attention from comparative psychologists.

It appears reasonable that the amount of information which can be stored in a mechanism of a given type would be limited by the size of that mechanism. Since the chimpanzee's brain has about one-third the mass of man's, its capacity for concurrent learning (and retention) may well be smaller. This is only an inference, however, since the associative abilities of laboratory primates have commonly been tested only in terms of isolated, individual items.

Actual measurement of information capacity, in this sense, is presumably impossible; and the closeness of an approximation might well be limited by such practical matters as the *S*'s life span, and the nature of the sensory channels through which information can be transmitted. However, it is not unreasonable to assume that the ultimate capacity of a species would be reflected in its ability to handle a smaller amount of information, of limited variety, in a short period of time. The present investigation was based on this assumption, and was designed to explore the experimental possibilities of concurrent learning, using the object-discrimination technique.

METHOD

Our principal *S*s were six chimpanzees that had recently served in a study of discrimination learning set (1) and had attained a high level of proficiency in the learning of individual object-discrimination problems. Except for the differences noted below, our general procedure was the same as that used in the preceding study.

Concurrent discrimination procedure. In this experiment, a *problem* involved not one pair of objects, but 5, 10, or 20 pairs. A *trial* consisted of the presentation of all the pairs in a given problem, in succession. One trial followed another immediately, with no break in procedure, the beginning of the second trial being distinguished from the end of the first only by the reappearance of an old pair of objects. The order of presentation of pairs within a problem was ordinarily held constant from trial to trial; however, this was merely a matter of convenience, for the serial position of a pair provides no cue to correct choice. (We have occasionally scrambled the order on successive trials, without affecting the *S*'s performance.)

Five-pair problems were run for 5 trials; 10- and 20-pair problems were run for 3 trials. Subjects were given one problem at a session, which thus involved 25, 30, or 60 choices. From 25 to 60 of these multipair problems were used with various *S*s. In general, the shorter problems were used first and the longer ones last, but there were numerous exceptions to this order.

Although our purpose was to vary only the number of concurrent associations being learned in the three sizes of problem, our procedure introduced a related variation in the time interval between successive presentations of a given pair of objects. This interval ranged from about 90 sec. for 5-pair problems to approximately 6 min. for 20-pair problems. We have some data which indicate that trial spacing of this order has no great effect on the learning of single-pair problems, and we will tentatively assume that this factor is not important in the present work.[2]

The discriminanda were 600 previously described objects (1) plus 100 more of the same general type. No two of them were enough alike to be difficult to distinguish when seen at the same time, but there were many similarities which provided possibilities for confusion among them in memory. Because more than five hundred *pairs* of objects were used with some *S*s, it was often necessary to recombine previously used objects into new pairs, and use them again. Control tests have indicated that such re-use has no appreciable effect on performance.

Our procedure will be recognized as very similar to that referred to by Riopelle *et al.* (2) as "serial discrimination." (We have not adopted this terminology because it emphasizes an essentially incidental feature of the procedure, and because it has occasionally been applied to maze learning and to the multiunit discrimination apparatus often used with rats.)

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[1] This investigation has been assisted by grants from the American Philosophical Society and from the Samuel S. Fels Fund.

[2] Later work indicates that an intertrial delay of 60 sec. may cause an appreciable reduction in second-trial accuracy. It would have been better, therefore, to have kept the time interval constant in the present study.

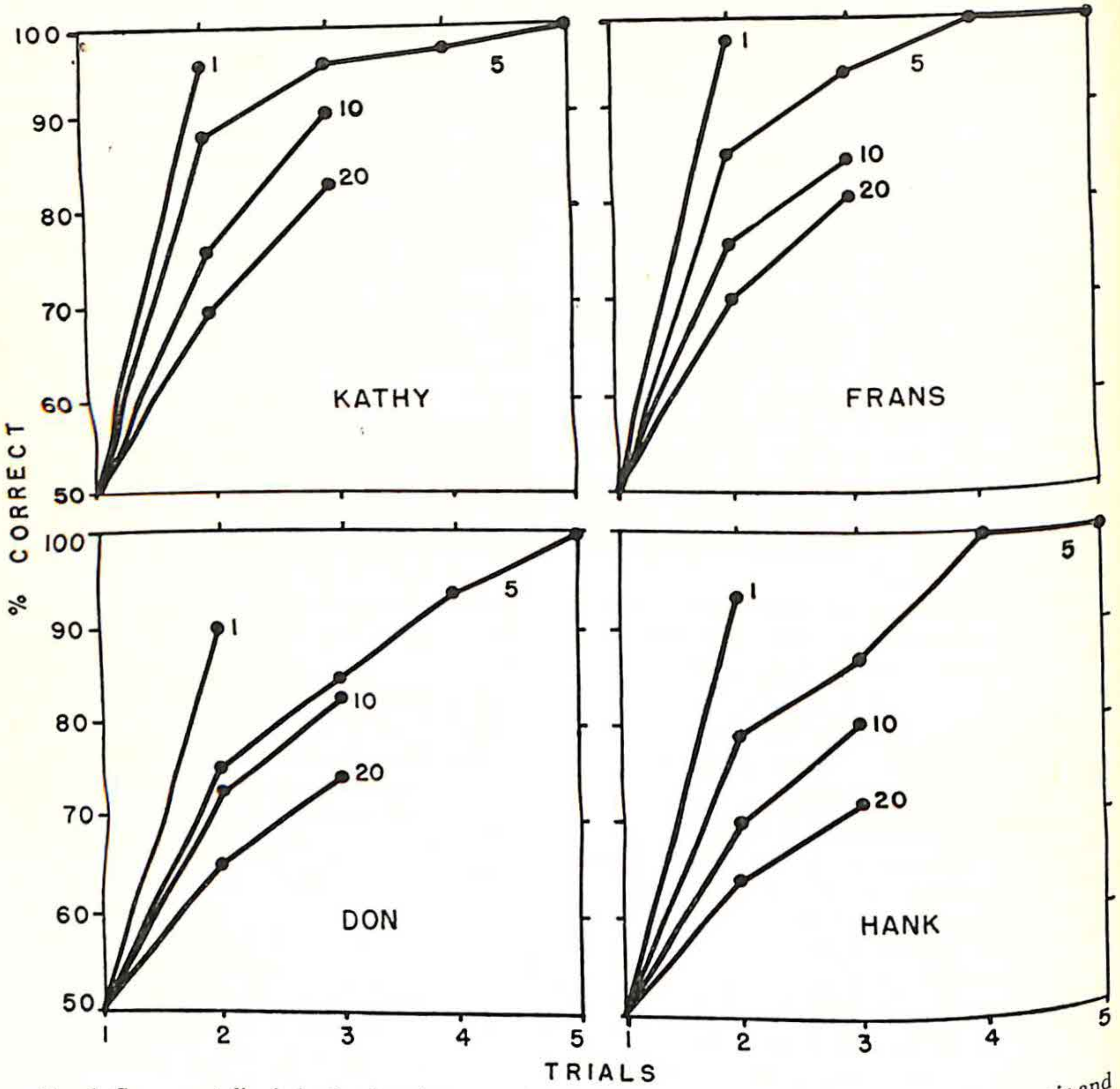

FIG. 1. Concurrent discrimination learning curves for the last 50 single-pair problems, the last 10 five-pair and ten-pair problems, and the last 5 twenty-pair problems

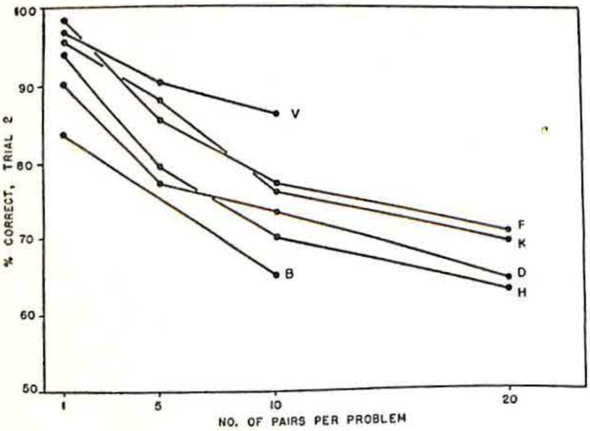

FIG. 2. Second-trial accuracy as a function of problem size. Individual subjects are indicated by their initials. Their ages, in years, were: Viki 4½, Frans 6, Kathy 2½, Don 17, Hank 7, Bokar 26.

RESULTS

Figure 1 shows how problems consisting of 1, 5, 10, and 20 pairs of objects were solved by four *S*s toward the end of their training. (The data for single-pair problems are from an earlier investigation [1].) The relative difficulty of problems containing various numbers of pairs is shown in Figure 2, in terms of second-trial accuracy.

Our data do not provide a clear picture of the development of a learning set for this kind of work—largely, no doubt, because our procedure was not designed for that purpose. There was some indication of improvement during early training on 5-pair problems, but much less during later 10-pair problems, and none during the 20-pair work. The superior performance of the home-raised chimpanzee, Viki, may be due to a pre-experimental learning set.

SUPPLEMENTARY WORK WITH NAIVE CHIMPANZEES

Dehn (7 yr.) and Dag (7 yr.) were each tested on two ten-pair problems without having previously been trained on single-pair discrimination. These problems were run to a criterion of two successive errorless trials (20 consecutive correct choices). The criterion was attained after from 10 to 14 trials. An average learning curve for the total of four problems would reach the 80 per cent level at about trial 10. This performance is not greatly different from that of naive chimpanzees on single-pair problems.

Although training on each of these problems extended over three or four days, there was little evidence of forgetting between sessions.

DISCUSSION

It is apparent from Figure 1 that the number of discrimination solutions a chimpanzee can retain simultaneously is a function of the amount of training given. Our problems were limited to a maximum of 20 pairs so that each one could be completed (if not mastered) in a single work session. However, since our two naive *S*s showed little intersession forgetting, it would apparently be quite practical to use problems of 50 or more pairs, with one trial per session. Extrapolation of the curves of Figures 1 and 2 suggests that a 50-pair problem might be learned to the 90 per cent level in something on the order of 20 trials.

Performance on concurrent problems would undoubtedly be a function of the type of discriminanda used. In the case of spectral hues, for instance, a limited number of discriminable stimuli would be available, and the interference among many of them would be extreme. In the present experiment, one test object might resemble another one in the same problem quite closely in color (*or* size, form, texture, etc.), but there was never simultaneous similarity in *all* visual characteristics, nor in the total configuration.

It seems unlikely that the sensory acuity of our *S*s was overtaxed by these objects, but their perceptual organization may have been. An *S* that learned only that the baited object was red might be confused on encountering another red (but unbaited) object, before the reappearance of the first one. This would be much less troublesome for an *S* that learned these objects as a large, rectangular, red one, and a small, round, red one. If the objects could be perceived as a brick and a rubber ball, there would be very little basis for interference. Utilization of this last type of perception may have been responsible for the superior performance of Viki, our home-raised chimpanzee. After four and one-half years in a human environment, she was quite familiar with many of the things used as test objects, or with the parts and materials of which they were made.

Figure 2 shows that our *S*s tended to maintain the same rank order in concurrent learning as they had previously attained in the learning of individual pairs. This suggests that concurrent discrimination learning may be thought of as demanding a higher degree of the same basic skills or abilities as are involved in simple discrimination learning. In the latter case, an object need be learned only well enough to distinguish it from the other member of the pair; in the former case, it must be distinguished from all the other objects in the multipair problem. Both cases are subject to proactive inhibition from the preceding problems, but concurrent learning is subject, in addition, to retroactive inhibition within each problem.

SUMMARY

Chimpanzees were trained on discrimination problems in which 5, 10, or 20 pairs of stimulus objects were presented in rotation. Accuracy as high as 80 per cent was attained on the third presentation of the 20-pair problems.

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TRANSFER SUPPRESSION AND LEARNING SETS[1]

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Progressive interproblem improvement in learning has recently been described by Harlow (3), using normal monkeys, brain-injured monkeys, and children. In the early stages of learning the percentage of correct responses on the second trials of a series of discrimination problems for normal monkeys was scarcely better than chance, but after they had attempted many such problems, the *S*s achieved more than 95 per cent correct responses on the second trials of these problems. This learning-to-learn was called the formation of learning sets.

Conceptualizations of these complex phenomena might well proceed along one or more of the following lines:

The supporting-habits theory. This point of view postulates that discrimination itself is basically very rapid or immediate but that successful performance in a particular apparatus depends in part upon the acquisition of certain supporting habits which are learned more slowly. Requisite orientational and emotional learning might be of this type.

The irrelevant-habits theory. This viewpoint similarly assumes rapid or immediate discrimination, but that proficient performance is not revealed until after the elimination of incompatible responses intrinsic to the test situation. Harlow (4) has analyzed a variety of such responses including perseveration, differential cue, response shift, and position-habit errors. This approach is related to the supporting-habits approach in minimizing the significance of the actual stimulus characteristics or interference between sequences of stimulus objects.

The transfer theory. This point of view implies that intraproblem discrimination is acquired slowly unless the responses to stimulus aspects of a given problem have been differentiated through experience with similar stimulus aspects of previous problems. The recent demonstrations by Lawrence (7, 8) of the "acquired distinctiveness of cues" might serve as a basis for an extensive exposition of this view. Hovland's (6) reference to learning-set studies as "successive transfer studies," however, was not necessarily as restrictive as this theory implies.

The stimulus-independence theory. We might further consider as a possible line of attack that the successive problems become more readily differentiated from each other and that responses to a particular problem eventually are not transferred to succeeding problems, i.e., the successive problems become independent of each other. This theory and the transfer theory both emphasize the importance of interproblem stimulus relations. They differ as to the role that interproblem transfer plays in determining proficiency of performance.

These possible approaches are not necessarily exhaustive or mutually exclusive. Neither are they direct descendants of particular formal learning theories. They are, however, potentially fruitful avenues for more formal theoretical excursions.

The specific aim of the investigation was to analyze the extent to which the responses to a given pair of stimulus objects would be elicited by the same stimulus objects presented again after a number of intervening problems. A progressive increase in the occurrences of such responses would support the transfer theory, whereas a progressively diminishing frequency would favor the stimulus-independence theory.

METHOD

Experimental Design

The experimental design is an extension of that used by Harlow, and it permits an analysis of additional factors intimately related to the formation of learning sets and interproblem transfer.

During the first day of testing the monkeys were presented with five six-trial discrimination problems. After completion of the five problems, the first or the fourth of these was presented again, but the reward

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[1] This investigation was supported in part by a research grant (MH-359) from the National Institute of Mental Health of the National Institutes of Health, Public Health Service.

values of the stimuli were reversed as in the discrimination-reversal procedure. This sequence was repeated on each test day. The animals were thus trained on five new discrimination problems and one reversed problem. A total of 378 problems (315 new, 63 reversed) was presented in this manner.

Subjects

Four adolescent rhesus monkeys participated in this experiment. They were tamed, accustomed to the test situation, and trained to solve six rather difficult preliminary discrimination problems requiring over two thousand trials for each animal. In view of the fact that object position was randomized in these problems, irrelevant position habits should have been stabilized. Furthermore, whatever supporting habits may have been required for successful performance on these problems should have been well established by this time.

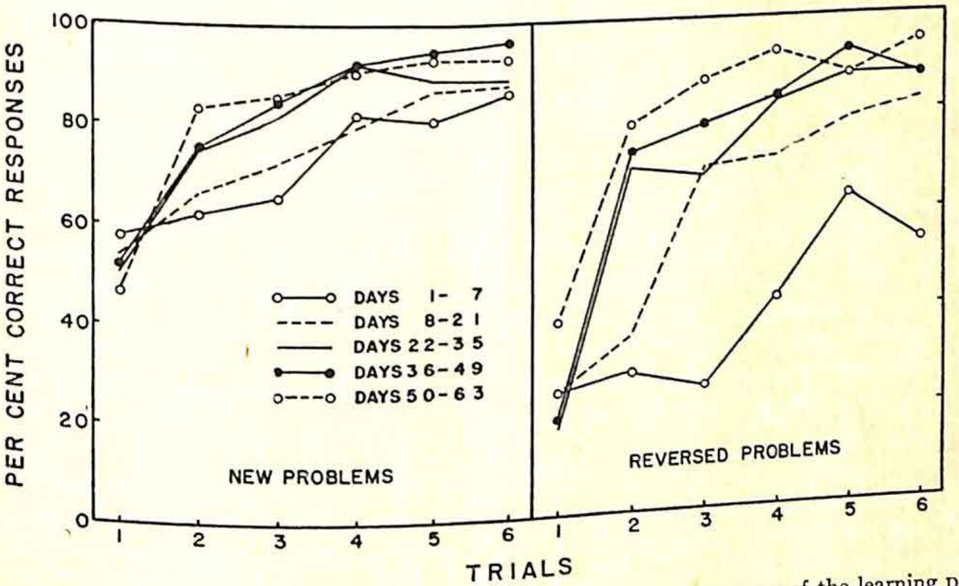

FIG. 1. Intraproblem learning for new and reversed problems at successive stages of the learning period. Left panel—new discrimination problems; right panel—reversed discrimination problems.

Apparatus and Procedure

Except for minor mechanical details the testing device was a duplicate of the Wisconsin General Test Apparatus (3, Fig. 1). The caged monkey faced a retractable gray tray bearing two test objects, each covering a food well. Of the 630 mutually different stimulus objects that were used, some were laboratory constructed, others were purchased, and the remainder salvaged from scrap heaps. Pairing of the objects and designating the correct member of each pair were accomplished with the aid of a table of random numbers. When the tray was pushed forward, the monkey responded by displacing one of the test objects. Displacement of the correct object resulted in reward for the animal; after an incorrect choice, however, the tray was immediately retracted. This noncorrection procedure was always used. Screens were employed appropriately to avoid experimental artifacts.

RESULTS

Transfer Suppression

The curves in the left panel of Figure 1 portray the change in the course of intraproblem learning through the series of 315 new problems. In the beginning of the series, the intraproblem improvement is nearly linear, but later the improvement between the first and second trials is greater than all the remaining improvement combined. This family of curves is similar to the curves presented by Harlow (3) and by Braun (1).

Similar changes in the forms of the early and late intraproblem learning are found in the reversed-reward problems, as shown in the right panel of Figure 1. In the early part of the training program there is negligible improvement between the first two trials and greater improvement in the later trials. With repeated experiences of comparable reversed problems, however, the location of the greatest increment in performance shifts forward until it eventually occurs between the first and second trial, and this single-trial increment becomes greater than all the increments of additional trials added together.

Figure 2 presents the percentage of correct responses on a given trial of the new discriminations in comparison with the corresponding trial of the reversed discriminations. Each of the six graphs portrays the changes for a given trial by blocks of seven days of testing. All points represent 140 choices for the new problems (seven days at five problems per day for four animals) and 28 choices for the reversed problems (seven days at one problem per day for four animals).

It is seen from these graphs that during the early phases of the experiment the performance on the reversed problems was substantially poorer than performance at the same stage of training of the new problems. During the course of the experiment, however, the differences in performance between the two classes of problems progressively diminished until eventually the trial 1 performances were similar and the performances on trials 2 to 6 were substantially identical.

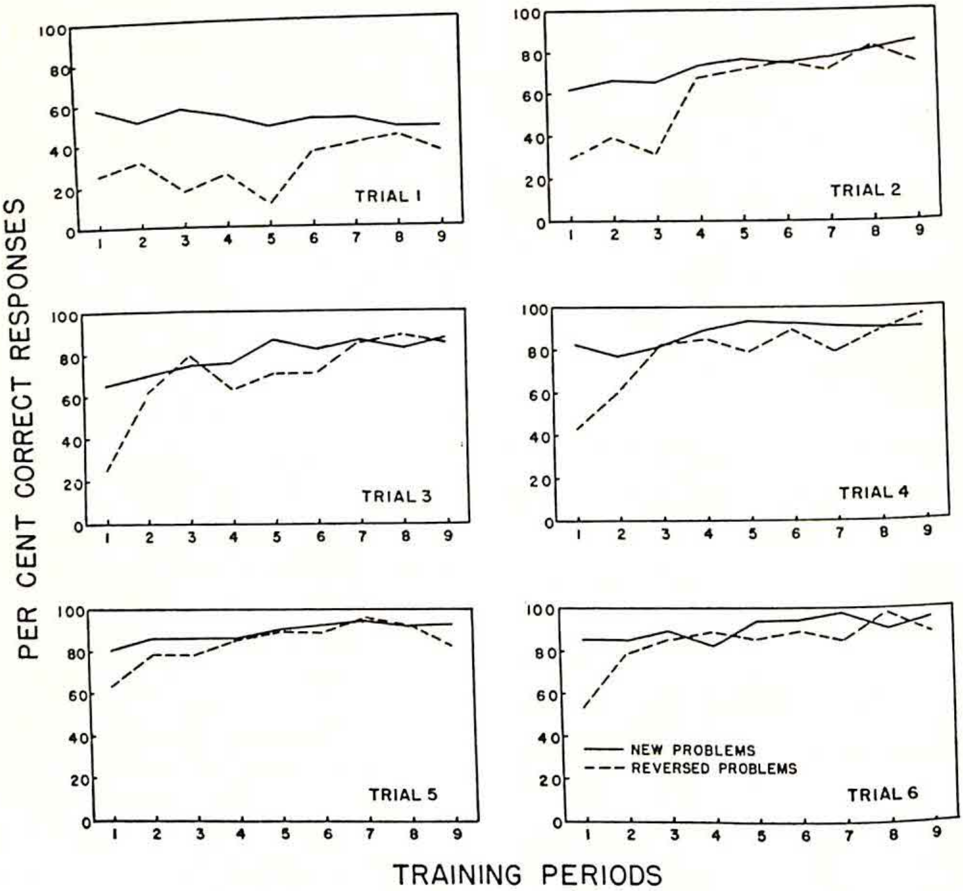

FIG. 2. Comparison of performance on specified trials for new and reversed problems at successive training periods

This retardation in performance on the reversed problems is a measure of the transfer effects from the animals' previous experience with the particular stimulus objects, and this negative transfer effect is most clearly shown on the first trial of the reversed problems. The dashed line of the panel for trial 1 shows that during the first 35 days (while the animals continue to improve in learning the problems on the initial presentation) the transfer effects increase slightly, and this results in a greater number of errors on the initial trials of the problems when they are presented a second time with reversed reward. After 35 reversed problems, however, there is a decrease in the transfer effects, which is reflected in the rise of the first-trial performance on the reversed problems. This improvement approaches, but in no case surpasses, 50 per cent. (A performance above 50 per cent would indicate spontaneous reversal of the previously presented discrimination problem.) Furthermore, the curves for trials 2 to 6 of the reversed problems do not reliably exceed those for the new problems, thereby precluding any delayed benefits of the previous experience. This decrease in the transfer effects during the later phases of the experiment occurs despite continued improvement in the original learning.

Intraproblem learning at two stages of training is illustrated in Figure 3. The left panel shows the marked difference in new and reversed problem performance during the first 14 days. About 30 percentage points separate the two curves. The right panel shows the same comparison for the last 21 days of training, and these curves are almost superimposable.

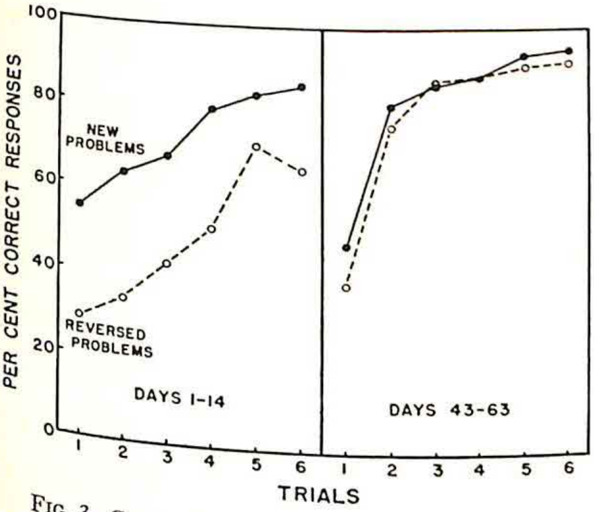

FIG. 3. Comparison of intraproblem learning for new and reversed problems at two stages of the learning period

Related Factors

Factors Involved in the Learning of Reversed Problems

Initial learning. Should transfer take place between the new and the reversed problems, a negative correlation would exist between the two performances for the same stimulus objects. If this transfer decreases, so should the size of the correlation decrease.

Separate correlations were computed for each animal between the number of correct responses on the original problem and the number of correct responses on the reversed problem for the first 21 days. The obtained correlations were −.70, −.53, −.20, and −.34. Comparable correlations for the second 21 days were either negative or near zero.

Intervening problems. The gradual reduction in the difference between learning a new problem and learning an old, reversed problem led to the interpretation of a suppression of transfer tendencies. Suppression of previously learned material by the learning of an intervening task has usually been considered in terms of retroactive inhibition. One of the well-known results of studies of this phenomenon (9) is that, to a great extent, increasing the amount of interpolated learning increases the amount of retroactive inhibition.

In the present experiment an evaluation of the effects of two amounts of interpolated learning is possible. On each day the first or the fourth problem on that day was reintroduced after the fifth problem, and the difference in performance on these two kinds of problems provides a measure of the effects of unequal amounts of interpolated learning. Figure 4 shows the percentage of correct responses on the reversed problem as a function of the problem reversed for three stages of training. The superiority of performance on the reversed first problems suggests that four interpolated problems suppress transfer more than does only one interpolated problem. Of paramount importance, however, is the fact that as training continues, the difference between the two inhibitory effects decreases until the two curves are practically identical. The upward slope of both these curves reflects the increasing efficiency with which the reversed problems are learned.

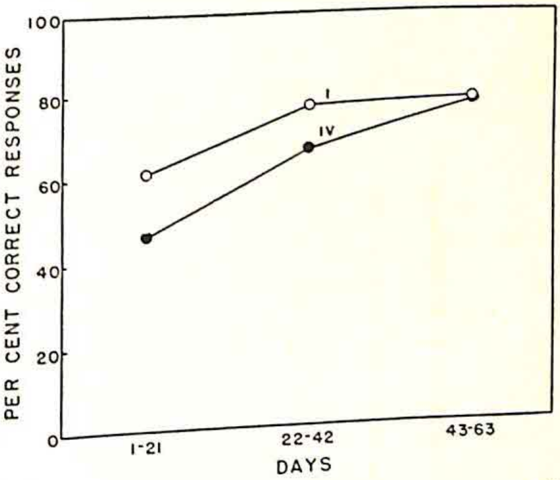

FIG. 4. Change in the effects of differing amounts of interpolated learning upon acquisition of reversed problems at three stages of training. Curve I indicates percentage of correct responses for reversal of first problem, whereas Curve IV denotes acquisition of the reversed, fourth problem.

Factors Involved in Learning Both New and Reversed Problems

Rewarding the initial trial. One of the error factors analyzed by Harlow was the stimulus-perseveration error. Errors of this type were defined as "... the excess of consecutive errors following a first trial error beyond those which would be predicted from the obtained frequencies of all errors" (4, p. 28). In the analysis of those errors Harlow found that late in learning the number of errors on trial 2 was less than would be expected but that errors on trial 3 and beyond were greater than expectation, yet a trial 3 perseverative error by definition depended on the occurrence of a trial 2 error. This peculiarity suggested to Harlow that other factors were operating. One such factor might depend upon the differential effects of rewarded and unrewarded initial trials, a differential effect such as that already observed by Moss and Harlow (10). It would be of interest to determine whether this phenomenon is altered by varying amounts of test experience. Furthermore, a comparison of such effects between the original and the reversed problems might reveal added factors which accompany transfer suppression.

The results of such an analysis averaged for 21 days of testing are presented in Figure 5. Parallel analyses were performed for the new and for the old, reversed problems. The left-hand portion of this figure shows the results for the new problems. The curve labeled $P+$ $(+)$ shows the probability ($\times$ 100) that a correct first trial is followed by a correct response on trial 2. It is seen that for this curve, correct first trials are followed approximately 70 per cent of the time by correct second trials. Regardless of the basis of these initial choices, they are, when correct, more likely than not to be followed by additional correct choices, and this likelihood remains constant despite an increasing percentage of correct responses on trial 2. The $P-$ $(+)$ curve gives the probability ($\times$ 100) that an incorrect initial choice is followed by a correct one. Unlike the $P+$ $(+)$ curve, the $P-$ $(+)$ curve rises and eventually reaches above 90 per cent. The relative effects of rewarding the initial trial thus change with increasing amounts of discrimination test experience. Not only does the magnitude of the difference change, its direction changes as well.

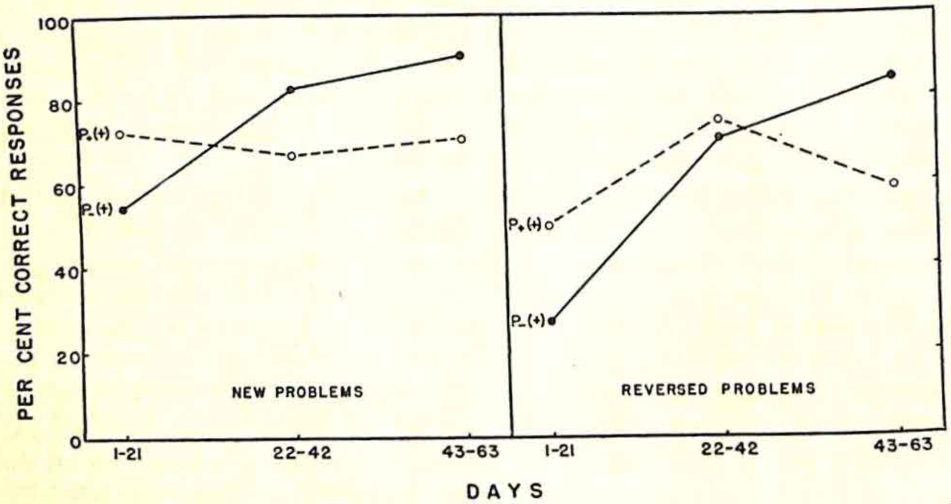

FIG. 5. The effects of rewarding the first trial of new and reversed problems at three stages of training. Curve $P+$ $(+)$ denotes the percentage of correct responses on trial 2 following a rewarded selection on trial 1. The $P-$ $(+)$ curve indicates the percentage of correct responses on trial 2 following an incorrect choice on trial 1.

Identical comparisons for the reversed problems are shown in the right panel of this figure. Broadly speaking, the same trends are seen. Furthermore, the terminal values for reversed problems approximate those for new problems.

Positional-response biases on initial trials. The nature of positional biases on the first trials of new problems has been analyzed, and the results of the analysis are presented in Table 1. Inasmuch as five problems were given each day, all values of the table are based on 105 choices. All but the three values nearest 50 per cent are significantly different from chance at well beyond the .01 level of confidence. The position habits of three of the animals are pronounced.

The trends of the results for the reversed problems were in all cases in the same direction as those presented in Table 1, but the departures from chance expectancy were less marked.

TABLE 1
Number and Percentage of Responses to Left Position on First Trial New Problems

ANIMAL	FIRST 21 DAYS		SECOND 21 DAYS		THIRD 21 DAYS	
	No.	%	No.	%	No.	%
RF-6	68	64.7	93	88.6	89	84.8
RF-7	38	36.2	33	31.4	41	39.0
RF-8	39	37.1	54	51.4	50	47.6
FT-1	58	55.2	73	69.6	75	71.4

DISCUSSION

The first portion of the results showed that interproblem transfer by animals with some pre-experimental test experience starts at a fairly high level, possibly increases, and finally decreases toward zero. Stated another way, as the animals receive increasing experience with discrimination test problems, the performances on successive problems become increasingly independent. The release from the effects of experience with previous problems produces maximal efficiency in solving new problems, even though the release itself develops from extensive experience with a great variety of problems.

It is possible to relate these results to a number of phenomena studied in other contexts. For example, the developing independence of successive problems may be attributable to the cumulative effects of proactive and retroactive inhibition. In another context, Tolman has related the learning set data to "generalized instrumental beliefs" (11), which are to be distinguished from concretized "hypotheses." Although the theoretical relations have not been published, this interpretation may involve "unlearning." Tolman and Krechevsky (12, p. 67) noted that the usual learning situation is in terms of the development of a specific hypothesis out of a more general means-end-readiness, and that the reverse process should be called "unlearning." They further suggested that possibly these two aspects of behavior obey different laws.

Analysis of the data has revealed four factors which accompany transfer suppression and the formation of learning sets. During the first phase of the experiment performance on reversed problems was negatively correlated with performance on the original problems, but the correlations approached zero with increased practice. The hypothesis of transfer suppression would predict such a trend, but the restriction in variance accompanying nearly perfect performance could also suppress the correlation.

The negative correlations demonstrate the persistence of preferences acquired during original learning for particular stimulus objects of reversed problems. Comparable stimulus-perseveration responses would be transferred from one discrimination problem to another. If strong, this transfer would result in immediate correct responses or stimulus-perseveration errors. If this transfer is suppressed, stimulus-perseveration errors would decrease, a phenomenon demonstrated by Harlow (4).

Investigation of the role of the amount of interpolated learning showed that the effects of two differing amounts approached a common value and that the resulting retroactive inhibition is subject to modification by learning.

Greenberg and Underwood (2) have described an experimental finding that is related to the results found here. They found that as human *S*s obtained successively more practice in learning and remembering verbal material, they learned each successive list of paired associates at an increasing rate, but they also forgot each successive list at a faster rate, at least if retention was for longer than 10 min. Greenberg and Underwood concluded that loss in retention with increasing practice was attributable to the cumulative effects of proactive and retroactive inhibition. Such cumulative effects, if unchecked, would result in rapid forgetting. Whatever the limit attained by the cumulative effects of retroactive and proactive inhibition, it is not sufficient to prevent the formation of either discrimination learning or discrimination-reversal learning sets.

The differential effect of confirmation or infirmation of the initial choice was seen to change throughout the experiment. Comparable changes occurred for both new discrimination and the reversed discrimination problems. Although absolute values differed at the beginning of the experiment, they were approximately equal at the end, a fact providing further indirect support for the hypothesis that eventually both new and reversed problems are learned in the same manner.

Moss and Harlow (10), using a slightly different technique, have experimentally explored the effects of rewarding the initial trials of successive problems. Their results are in substantial agreement with those obtained in the final phase of this experiment, and they related their results to investigatory tendencies following a correct choice. The changing effects found in this experiment suggest that such investigatory tendencies may possess properties of skills as well as of drives (5).

The positional tendencies of three of the animals were pronounced, but in spite of this the animals developed efficient learning sets. Since it is impossible to obtain a high percentage of correct responses and make a high percentage of position responses, these position preferences must be suppressed during trials 2 to 6 of succeeding problems. Animal RF-6, for example, made 99 correct responses on trial 6 of the last 105 problems. Even if we make the unlikely assumption that every one of the six errors was attributable to a position preference, the maximum number of left-position responses that could be made would be approximately 59 out of the 105 trials. Although these responses are suppressed during trials 2 to 6 of the problems, they nevertheless reappear on trial 1 of the succeeding problem. Despite the interpretation placed on these initial preferences, they are highly provisional in nature and are readily suppressed in favor of a response to the correct object.

SUMMARY

1. The present experiment was performed to evaluate the characteristics of interproblem transfer relations and other factors which are of significance for the formation of discrimination learning sets.

2. The discrimination-learning performance of four adolescent rhesus monkeys was observed for a total of 63 days, and on each day the animals were tested on five new problems, one of which was subsequently presented as a discrimination-reversal problem.

3. All monkeys improved in the learning of both new and reversed problems. Disparities in rates of learning the two types of problems progressively diminished with further training.

4. At the beginning of the experiment, the animals relearned the reversed problems more readily if four interpolated problems were given than if only one interpolated problem was given, but the differential effects decreased as training progressed until finally no difference could be ascertained.

5. Rewarded initial trials of new discrimination problems resulted in 70 per cent correct responses on trial 2, and this percentage remained constant throughout the experiment. Unrewarded responses on initial trials were followed 55 per cent of the time by correct responses on trial 2 and this value rose eventually to reach 90 per cent correct.

6. No single positional bias was seen to develop, but the course of first-trial positional biases was found to be characteristic of particular animals.

7. The results were interpreted in terms of a suppression of interproblem transfer tendencies and of factors which accompany it.

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DEPRIVATION OF VISUAL FORM DEFINITION IN THE RING DOVE.
I. DISCRIMINATORY LEARNING.[1]

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Introduction

Deprivation of visual function throughout life is of interest to psychologists because of the relevance of the effects of this deprivation to theories of visual perception. Deprivation experiments have direct bearing upon the perceptual theories of Hebb (2), Köhler (3), Köhler and Wallach (4), and Lashley (5).

The method of deprivation heretofore employed has involved rearing the experimental animals in complete darkness from birth to time of testing. This method of rearing has been criticized because of the possibility that visual brightness deprivation in addition to visual form deprivation may initiate either retinal or central nervous structural changes. This objection has been partially confirmed by some findings of Riesen (6).

The usual method of dark-rearing was therefore modified in the present experiment so as to allow the retinas of the experimental animals to be continually stimulated during daylight hours by diffuse light, while, at the same time, perception of visual form was prevented.

SUBJECTS

The *Ss* were 36 ring doves from the colony maintained by the Department of Animal Behavior of the American Museum of Natural History. Of these, 24 experimental birds were reared without visual form definition, and 12 control birds were normally reared.

APPARATUS

A modified Lashley-type jumping apparatus was used in the training situation. Essentially this apparatus consisted of a perch so built that a bird upon it could "see" both stimuli located 20 in. subrostrally. The stimulus plates were so arranged that when a bird jumped down to the negative stimulus, the platform holding the stimulus collapsed, causing the bird to fall into a net 18 in. below. The stimuli were a frosted-glass triangle and a frosted-glass circle of equated area, both of which were on black backgrounds. The central area of each of these was illuminated from below by a 10-w. incandescent electric bulb. The walls of the jumping apparatus were painted flat black, and inasmuch as the experimental work was carried out in a darkened room, the only "figures" visible were the uniform fields of the circle and triangle. In the mid-line, posterior to the perch, the plunger apparatus of a pinball machine was set so that a jump could be forced on any bird which failed to jump in the time allotted for each trial. The inner edges of the stimuli were separated by 1½ in. Thus, it was impossible for the birds to make mid-line landings. The jumps were focalized and confined to the stimulus fields by having the front and sides of the apparatus flush with the edges of the stimuli, and by having the back of the apparatus as close to the perch as possible. Into the door, located at the top of the apparatus, was cut a small, rectangular observation window.

METHOD

The general sequence of operations in this experiment was as follows: *rearing* under conditions of visual form definition deprivation; *preliminary training* in jumping from a perch to the horizontal; *training* on a circle versus triangle discrimination; *testing* for visual acuity, and the checking of indices of the vestibular responses and the general health of the birds.

Conditions of Rearing

Because the eyes of the ring dove open when the bird is four to five days old, the experimental birds were hooded at three days of age with a plastic (vinyl) translucent head covering. This allowed the retinas of the squab to be stimulated thenceforth by a diffuse uniform field of light, but at the same time prevented form perception.

The transmission characteristics of the material out of which the hoods were cut were examined by two independent observers on a Bausch and Lomb constant-deviation spectrometer. Both observers agreed that the material was nonselective. All wave lengths passed through. There was no absorption even at the ends of the spectrum, where absorption most frequently takes place.

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[1] This paper is based on part of a dissertation submitted to the faculty of the Department of Psychology of New York University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The author wishes to express thanks to Dr. T. C. Schneirla for methodological and theoretical comments and criticisms from the initial planning stage to the final report of these experiments. Gratitude is also expressed to the Department of Animal Behavior of the American Museum of Natural History for the use of its experimental facilities.

[2] Now at the Institute for Research in Human Relations, Philadelphia.

The hood was fitted by hand and so designed that it allowed the beak of the young dove to extrude. This permitted feeding and breathing, while, at the same time, it prevented all specific form perception. The hood was also constructed so that it could be loosened, without ever being removed, to allow for growth of the bird. Hoods were inspected twice daily, and appropriate adjustments were made as needed. The hood was constructed so that it did not press against the corneas of the squab.

Owing specifically to the deprivation of visual definition, the doves did not develop pecking responses. Therefore, from the time of rejection by their parents until the termination of the experiment, the doves were fed and given water by hand. The same formula of mixed grain given to the normally reared doves (control animals) in the museum colony was fed by hand to the hooded birds. The feeding was accomplished by grasping a dove by the beak with one hand and inserting the food into its mouth with the other hand.

The control animals were reared normally in the museum colony. No experimental or control bird was younger than 8 weeks of age, nor was any older than 12 weeks of age when started on the preliminary training.

Preliminary Training

In advance of their use in training and tests, all experimental and control birds were given experience in jumping from a perch to a table top. This experience was essential for participation of the hood-reared birds in the training proper owing to their diminished "life style." It was observed that the hood-reared birds did not move about as much as did the normally reared birds, did not fly unless forced to do so, and when first unhooded as adults, were apt to fly only erratically and with definite errors in space orientation.

This pretraining was accomplished by use of a perch of adjustable height. Each bird was first forced to jump 20 times from a perch 2 in. above a surface. On the following day, the height of the perch was increased to 3 in., and the birds were given 20 trials at this height. This procedure was repeated daily. That is, each day the birds received 20 more trials, and the height of the perch was increased 1 in. At a height of 20 in., two days' training (or 40 jumps) was given. The total number of pretraining jumps each bird received, therefore, was 400.

Training

Following the pretraining, a window the size of the lower half eye was fixed in the mask of each experimental bird, thus allowing monocular vision. (For one group, trained using both eyes, two openings were cut.) Between experimental sessions this window was thenceforth covered with masking tape. Images of objects located subrostrally to the birds would impinge on the upper retina. Images of objects located suprarostrally would impinge on the lower retina. The *E*'s aim in covering the upper half eye and locating the images subrostrally was to confine images to the upper retina. Hence, when the terms "uncovered eye" or "eye" alone are used in this paper, it should be kept in mind that images were confined to the upper hemiretina. This restriction was not pertinent to the present experiment, but was introduced for the purposes of a further experiment with the same experimental birds.

Specifically, each experimental session for each bird involved the following routine. The bird was taken from a home cage in a blacked-out room and the appropriate aperture fixed for the eye to be uncovered during the experimental session. The bird was then placed in a blacked-out cage. Five minutes later the bird was taken from this blacked-out cage and was placed, via the door located at the top of the jumping apparatus, on the perch of the blackened apparatus. Before this, the stimuli had been set in place, and when *S* seemed comfortably perched, the stimuli were illuminated.

If the *S* made the correct choice (i.e., responded by jumping to the positive stimulus), the apparatus was immediately darkened, and the bird was then replaced in the blacked-out cage. Necessary adjustments, such as transfer of the position of the stimuli, were then made, and after an interval of 5 min., the bird was replaced in the apparatus, as above, for his next trial.

If the *S* made the wrong choice (i.e., responded by jumping to the negative stimulus), the stimuli were immediately darkened, and the bird was left in the net while necessary adjustments were made in the position of the stimuli. Immediately following these adjustments, the bird was replaced on the perch for its next trial. Hence, *S* was kept in the apparatus until the correct choice was made. Avoidance of the fall and return to the blacked-out cage following reaction to the positive stimulus thus constituted reward, and the fall following reaction to the negative stimulus constituted punishment.

If any bird failed to jump after 3 min. in the situation, the plunger apparatus was released, forcing the subject forward and off the perch, down to the stimuli.

Each bird received 30 trials per day. On completion of 30 trials, the hole in front of the eye used in training was covered with the masking tape and the bird returned to its home cage. The normally reared birds were treated in exactly the same manner in the experimental situation. However, the normally reared birds, for purposes of adaptation, wore hoods for three days in their home cages prior to being placed in the experimental situation, as well as during all experimental situations.

The arbitrary criterion of having learned the discrimination was nine out of ten consecutive jumps toward the positive stimulus on any one day of the training session. According to this criterion, if a bird jumped to the positive stimulus for its last eight trials on one day, it was still required to make nine out of ten consecutive jumps toward the positive stimulus on the following day.

Eighteen of the experimental birds were trained using their right eyes (Group A), and six were trained using their left eyes (Group B). Six of the normally reared birds were trained using their right eyes (Group C), and six were trained using both eyes (Group D). The number of subjects in Group A was greater than the number of subjects in the other groups because

Group A is a composite of birds used also in an additional experiment. Likewise, Group D, not a direct control for the present experiment, is included because of its relevance and interest as an indirect control.

Feeding of the birds of all groups took place after the daily experimental session.

PRECAUTIONS AND CONTROLS

Visual Acuity and Ophthalmoscopic Examination

Visual acuity was tested by taking advantage of the optokinetic reaction. When a drum consisting of black and white stripes is rotated in the visual field, doves and many other animals show nystagmic movements of the head. In testing visual acuity, the method of limits was used. That is, the width of the black stripes was decreased by 1-mm. steps until the optomotor reaction disappeared (upper threshold). Then, starting at a point below this, the width of the stripes was increased until the reaction reappeared (lower threshold).

TABLE 1

Trials for Initial Discriminatory Learning, Experimental and Control Groups

GROUP	*N*	EYE USED	MEAN	SIGMA
A	18	right	126.0	20.2
B	6	left	127.6	18.5
C	6	right	72.3	13.4
D	6	both	83.1	16.3

Three decreasing and three increasing series were given to each bird tested. The absolute threshold was defined as the mean of the three upper and three lower thresholds. Eight randomly chosen hood-reared birds and four randomly chosen control birds were so tested for visual acuity.

Six randomly selected birds, i.e., three normals and three controls, were examined opthalmoscopically to ascertain the condition of their retinas.[3]

General Controls

To exclude the possibility that some animals might learn from the manner in which they were placed on the perch or in dependence upon the noise made by the shifting of stimuli, the same kind of noise was made between trials whether the stimuli positions were changed or not, and *E* attempted to place *S* on the perch in exactly the same position and manner for each trial.

Varying the position of the positive and negative stimuli from right to left, following Gellermann's (1) series, controlled positional habits and the possibility that animals might react to relative distances of the stimuli from the side of the apparatus. For one-half the birds, the circle was the positive stimulus; for the other half, the triangle was positive. This evenly distributed over the data any innate propensity of the birds for either the circle or triangle, and also reactions made on the basis of brightness per unit area. This last factor was further controlled by varying, in a prearranged manner, the brightness of the positive and negative stimuli over four different levels as soon as a bird had made four out of four, or four out of five, reactions to the positive stimulus. Thus, each stimulus was brighter than the other for a portion of the last five or six jumps prior to the reaching of the criterion. This variation was continued until the bird either reacted twice toward the negative stimulus, or reached the criterion of mastery. If either the criterion of learning was reached or two incorrect jumps were made, the 10-w. intensity level was reinstated.

Animals may sometimes react to some minute aspect of the stimulus, rather than to the form of the stimulus. In order to control any cues, subliminal for human beings, to which the birds may have reacted, three different triangles and three different circles, all of the same dimensions, were used successively in a random manner in all experimental conditions for each bird.

TABLE 2

Comparison of *t*'s between Experimental and Control Groups

NORMALLY REARED	HOOD-REARED	
	A	B
C	6.97	5.30
D	4.87	4.04

RESULTS

In order to test the significance of the difference between the number of trials taken by the normally reared and hood-reared birds, Cochran's procedure recommended for use when there is suspected heterogeneity of variance was followed. The *t*'s derived from this method of treatment are presented in Table 2, and the means and sigmas for each group are shown in Table 1. The results indicate that in the four possible comparisons between hood-reared and normally reared groups in the initial training, the hood-reared groups took significantly more trials to reach the criterion than did the normally reared groups.

On the other hand, between the results for the two normally reared groups no significant differences are found. Similarly, between the two hood-reared groups, there are no significant differences. Therefore, the scores for the hood-reared birds were combined into one inclusive group. The same was done for the normally reared birds. This gave an inclusive mean of 126.8 jumps to reach the criterion (sigma, 24.9) for the hood-reared birds. The inclusive mean obtained for the normally reared birds was 77.7 (sigma, 15.9) trials. This difference is significant below the .01 level.

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[3] Drs. H. L. Teuber, S. Weinstein, and J. Semmes performed the opthalmoscopic examination of the birds.

No statistically significant difference was shown between the visual acuity of those hood-reared and those normally reared birds tested. Here we follow the general assumption that the optokinetic test is valid for appraising visual acuity. This statistical comparison was confirmed by postexperimental observation of the hood-reared birds.

Opthalmoscopic examination indicated a limited opacity of the fluid media of the eyes of the hood-reared birds as compared with the normally reared birds.

No gross behavioral differences to rotary acceleration and deceleration were noted between the experimental and control groups.

DISCUSSION

Several alternative explanations may be submitted for the larger number of trials taken by the hood-reared birds to reach the criterion of learning the visual discrimination used in this experiment.

In view of the opthalmoscopic data, it is possible that diminished visual acuity in the hood-reared birds operated to cause the increase found. The present author tends to reject this as the crucial variable because the visual-acuity data of the hood-reared, as compared with the normally reared, birds did not support this, and because the postexperimental hood-reared behavioral emergences, which depend upon a functional visual substrate, were not such as to support this explanation. For example, 15 hr. after having been unhooded, the hood-reared birds demonstrated coordinated pecking at small grains of food. Various other explanations in terms of central nervous changes, retinal degeneration, and photochemical imbalance, are also rejected in view of the demonstrated visual function of the hood-reared doves. Specifically, it does not seem that these chemical or physiological changes, if present, would reverse themselves within the time that the above-mentioned coordinated responses, which depend upon a functional visual system, emerged. Attributing the discriminatory learning shortcomings of the hood-reared birds to some motor or structural deficit imposed by hood rearing seems also unacceptable on the grounds that close observation of the hood-reared birds brought out nothing to support this explanation, and also on the grounds that pretraining to jumping seems to have controlled this variable. The essential motor response, jumping from a perch to the horizontal, seems to have been established in the habit repertoire of the hood-reared birds by the pretraining. Moreover, the hood-reared birds were able to fly nonerratically after a period of one to two days in a cage permitting flight in spite of the diminished "life style" imposed by hood rearing. This would indicate not only a healthy, mature motor substrate, but also a visual substrate that could function in terms of an adequate perception of objects after the appropriate learning had taken place. That the pretraining may have been differentially effective for the normally reared as compared with the hood-reared birds also seems unacceptable on observational and operational grounds. It can be stated that the conditions of learning during the pretraining, as well as during the training and testing sessions, were as equivalent as possible for the hood-reared and normally reared animals. To the criticism that unrevealed qualitative differences may have existed in the effectiveness of the reward for the experimental and control groups, the investigator can only point to a too slender evidence regarding the role of differential effect in the early stages of perceptual-motor learning. If there actually was a differential effect from falling on the development of the perceptual processes in our experimental and control cases, further investigation is required to demonstrate it.

We therefore interpret our results as supporting theories which emphasize experience as a prerequisite to normal adult function in visual perception. The crucial variable would seem to have been the visual inexperience of the experimental animals.

The perceptual theory of Hebb (2), or that of Köhler and Wallach (4), might have predicted the present results.

SUMMARY AND CONCLUSIONS

Twenty-four ring doves were reared to the time of investigation without experience in visual form definition and were so maintained between training jumps and sessions. The number of trials taken by these birds, as adults, to learn a visuomotor perceptual task was then compared with that of 12 normally reared birds. The birds reared without visual form definition took significantly longer to reach the criterion of learning than did the normally reared birds. This finding is interpreted as being in conformity with perceptual theories which maintain that a change in the neural substrate, dependent upon previous visual experience, is a prerequisite for normal adult visual function.

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THE EFFECT OF ANXIETY—A PROBLEM IN MEASUREMENT

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One of the recurring problems in psychology is the question of the gross effects on behavior of anxiety, emotion, or severe physiological disturbances due to brain ablation, electroconvulsive shock, or the administration of drugs. The sort of question that often arises is whether behavior under the experimental conditions is more or less "well integrated" than normal, or whether specific behavior patterns have actually been affected by the experimental operations. Often the objective evidence—error scores, time scores, and so on—says no, but E feels that there *is* a difference in performance. In other cases, the behavior of the animal is markedly different but it is difficult to describe just what the difference is, and E must resort to moving pictures or literary description.

It is the purpose of this paper to illustrate, by an experimental example, a descriptive technique that appears to be extremely sensitive and may enable us to quantify certain kinds of complex behavior that, at present, necessitate an essentially clinical description. The experiment involves the establishment of what has been called an anxiety-producing stimulus (1). The problem is to determine the effects of such a stimulus on behavior.

METHOD

Subjects and Apparatus

Six male albino rats, approximately 120 days old, were divided into two groups—experimental and control.

Both groups were run in an apparatus that has been described in detail elsewhere (2). It consisted of a modified Skinner box in which the food tray and the bar were at *opposite* ends of the cage. A photoelectric cell system made it possible to record approaches to the tray as well as the usual bar-pressing responses. For the present experiment the box was further modified by the addition of an electric grill in the floor and sheet metal siding (to prevent shock avoidance by climbing). The experimental box was in a dark, sound-treated chamber with recording and control apparatus outside.

Procedure

Prior to the experimental test each animal was placed in the experimental situation for two 12-hr. periods, spaced three days apart. A 25-w. light located at one side of the cage was turned on occasionally during this adaptation period. For the three rats of the experimental group this light was always accompanied by electric shocks of 5- to 10-sec. duration, severe enough to elicit jumping and squealing. The light was left on for varying periods of time and the shock occurred several times during the light interval. The light-shock schedule was not systematic but was maintained until a reasonably clear clinical picture of anxiety ("freezing," trembling, defecation) was observed in the presence of the light. The control group was also exposed to random light periods, but no shock was given.

On the day following the completion of this adaptation and conditioning procedure, each animal was returned to the experimental chamber at its scheduled feeding time. The light was out, and an automatic feeder had been connected to the bar. Each animal remained in the situation until it had obtained 100 regular reinforcements for bar pressing. Three more sessions of 100 regular reinforcements were given on succeeding days.

On the final day, each animal was run through the following test schedule (symbols are those used in Fig. 1).

(I_a) 10 min. of regular reinforcement with light on
(RR_1) 8–12 min. of regular reinforcement in the dark
(I_b) 8–12 min. of regular reinforcement with light on

The experimental group received no shock during the first light period (I_a) and one shock of 2-sec. duration during the second light period (I_b). The control group, of course, received no shock. The actual time in the light and the dark varied somewhat for each animal, depending on its rate of reinforcement. (It was necessary to limit each animal to 100 reinforcements to prevent satiation effects.)

Treatment of the Data

The apparatus mechanically defines two responses that can be symbolized A (Approach to food tray) and B (Bar press). The data appear as ordered sequences of responses: $ABAABABA\ldots$ representing the animal's course of action, or pattern of behavior during the period of observation. A sequence of this sort may be correlated against itself and this operation repeated a number of times, each time with the sequence displaced a constant amount (m). Such a procedure yields an auto-correlation function. (For computational details see reference 2, pp. 33-35.) In the present case, the constant of displacement was a single response, and we, in effect, determine the correlation of each response with its successor, second successor, and so on.

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[1] The work reported here was done at the Psychological Laboratories, Harvard University. It was reported in part at the 1950 meetings of the Eastern Psychological Association. The author is indebted to Mr. N. D. Squires for the actual carrying out of the experiment.

The resulting function yields a simple quantitative description of the pattern of the animal's behavior. The *degree* of patterning is reflected in the rate of attenuation of the function. The *form* of the pattern is reflected in the form of the function.

RESULTS

The results of the experiment are presented in Figures 1 and 2. Figure 1 presents the auto-correlation functions for each rat in the experimental group. The functions labeled *RR* are from the last 200 responses made under regular reinforcement in the dark on the day prior to the experimental test. The remaining functions are obtained by separately plotting responses made during the first light period (I_a), the intervening dark period (RR_1), and the second light period (I_b).

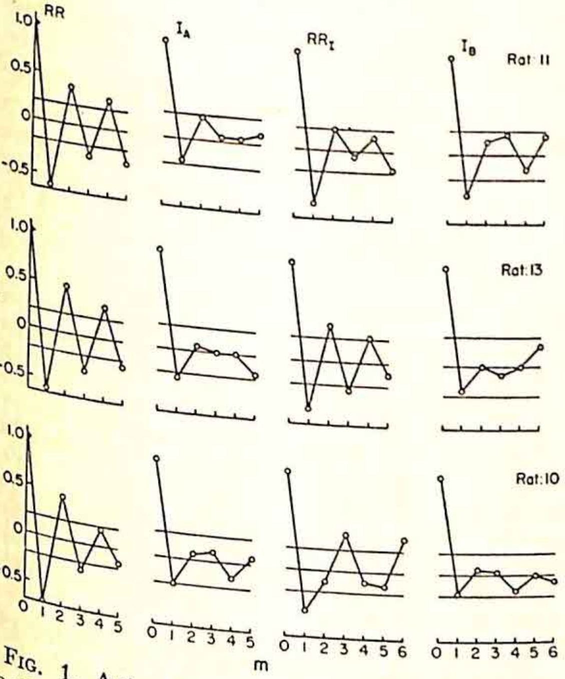

FIG. 1. Auto-correlation functions of data from experimental group. The horizontal lines represent the .05 fiducial limits based upon the hypothesis that $r = 0$. Symbols are explained in text.

As might be expected, the large number of regular reinforcements before the test established a well-organized alternation of responses to the bar and the food tray. This is indicated by significant positive correlations for even values of *m* and negative correlations for odd values of *m*. The strength (or stereotypy) of the pattern is quite high, as indicated by the relatively slight attenuation of the auto-correlation function. Correlations are still significant after three to five displacements.

In the presence of the light (I_a and I_b), this pattern of behavior is disrupted. There is still some tendency to alternate responses, as indicated by the negative correlations between each response and its immediate successor. The amount of patterning is, however, markedly lower. The response sequence is very nearly random.

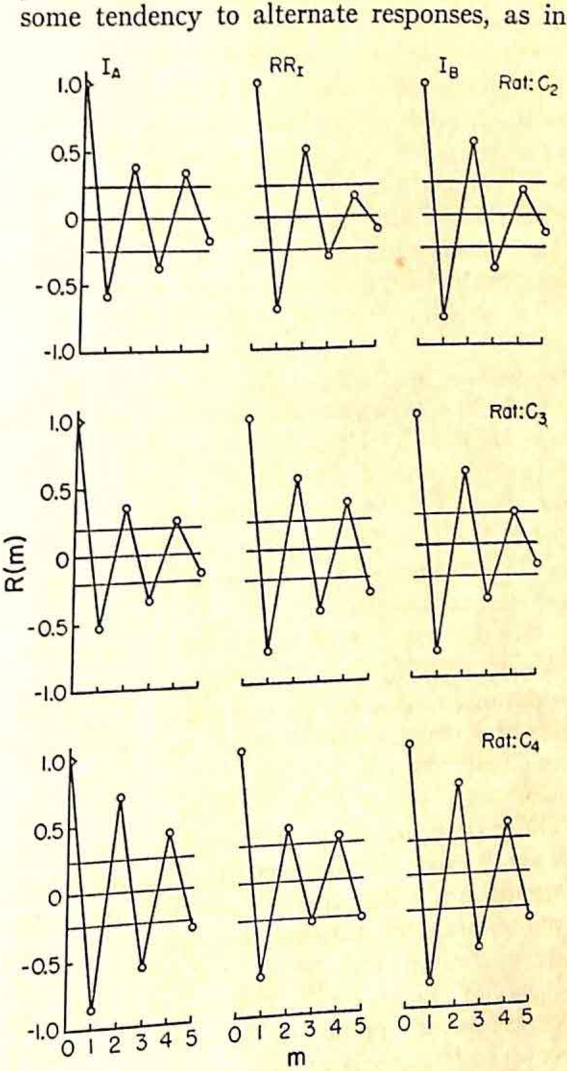

FIG. 2. Auto-correlation functions of data from control group

That this disorganization of behavior is due to the earlier association of shock with the light is clear when the functions presented in Figure 1 are compared with the same functions derived from the control-group data and presented in Figure 2. To avoid redundancy,

RESPIRATORY CHANGES DURING THE CONDITIONING OF FISH

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That fish of different species can develop associations or conditioned responses to a variety of stimuli is a well-established fact. The frequently cited experiment of Triplett (10), reported in 1901, showed that such a fundamental reaction as the striking or feeding response in perch could be broken down by the proper reinforcement and that an inhibition could be set up in its place. Differential conditioning in the visual modality was successfully demonstrated by Washburn and Bentley (11), who trained the creek chub to discriminate between pairs of colored forceps. And auditory or vibratory conditioning is illustrated in the investigations of Frolov (6) and of Harlow (7), both of whom used electric shock as the unconditioned stimulus.

A series of studies on marine fishes by Bull (1, 2, 3, 4) has employed the conditioning technique to measure such things as the sensitivity to temperature and salinity changes in the water, and the reactions to monochromatic lights as contrasted to closely allied shades of gray. Fish have even been reported to be capable of second-order conditioning (9).

It was the purpose of the present experiment to probe further into the nature of learning or conditioning in fishes, partly because of the primitive development of the forebrain in these animals and the absence of the cerebral cortex (8). Specifically we wished (*a*) to compare the respective rates of conditioning to visual and to audiovibratory stimuli, and (*b*) to see what relationships, if any, might exist between the rate or efficiency of learning and the "emotional condition" or "anxiety state" of the organism as determined by its rate of respiration. The striped mullet, *Mugil cephalus* (L), an extremely fast swimming and excellent salt-water food-fish, was selected as the subject for investigation. The research was conducted at the Marine Laboratories of Florida State University on the Gulf of Mexico.

METHOD

Apparatus and equipment. Twenty-four striped mullet, divided into three equivalent groups of eight fish each, which will hereafter be designated as the Bell (B), Light (L), and Extinction (E) groups, were used in the research. All fish were between 8 and 11 in. in length. Each animal was conditioned individually, in a conditioning compartment, 42 in. by 12 in., which was partitioned off within a larger glass aquarium. The water level in this compartment was maintained at a depth of 11 in.

The rear wall of the conditioning compartment consisted of a ¼-in. marine-plywood panel. Rigidly fastened to this panel above the water line was an ordinary doorbell. The plywood partition acted, therefore, as a sounding board and could be used to transmit auditory or vibratory stimuli into the water. This was the source of the conditioned audiovibratory stimuli employed in the present study.

The source of the conditioned visual stimulus was a 100-w. frosted electric light bulb, mounted outside of the tank in a gooseneck study lamp. The lamp was adjusted to shine horizontally into the end of the conditioning compartment, through the glass wall of the aquarium.

The unconditioned or reinforcing stimulus was a d.c. electric shock sent through the water of the tank by six ¼-in. vertical brass rods—three at each end of the conditioning compartment. The source of the current was a rectifier which delivered a shock of 6 v. and 2 amp. at the electrodes.

The experimenters and apparatus were completely screened from the aquarium tank, and all observations were made through a 3-in. by 12-in. slit in the screen.

Conditioning procedure. The stimuli were timed by a .01-sec. electric time-clock so that the conditioned stimulus lasted for 3 sec. and the unconditioned stimulus overlapped the conditioned for the final 1 sec. of the 3-sec. period. The massed method of training was used, with the interval between successive trials varying from 30 sec. to around 2 min. Unreinforced control trials presented before the training was begun gave an indication of the original or natural effectiveness of the conditioning stimuli.

Each subject was run through the acquisition and extinction procedures in from 2 to 3 hr.—depending upon whether extinction was given. A pilot study conducted before the main experiment had demonstrated that conditioned behavior of the generalized sort elicited in the present situation could be obtained, to a criterion of 10 successive CR's, within 70 training trials or less. As a consequence a trial-limit criterion of 70 training trials was adopted. Every regular conditioning trial was reinforced, so that the method was that of classical or Pavlovian conditioning rather than instrumental conditioning.

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[1] Contribution No. 5 from the Florida State University Oceanographic Institute.

The eight animals in group E were introduced after the training of groups B and L in order to measure the strength of the CR by the extinction method. Four fish in group E were conditioned to the bell and four to the light stimulus. After the completion of their original conditioning, each individual was then given nonreinforced or extinction trials until the criterion of 10 successive trials without a CR had been attained.

The measurement of respiration. Respiration rates were taken for all subjects during each phase of the experiment. The method of recording respiration was to count the mouth or gill movements for 15-sec. periods beginning 10 sec. after the termination of each trial. Two observers collaborated in making these counts. If a difference occurred between them, which was very rarely, the average score was taken for the 15-sec. period in question.

RESULTS AND DISCUSSION

Kinds of responses observed. There were three sorts of responses to the stimuli presented which were clearly in evidence—each distinct and differentiable from the others. These were (*a*) the preconditioning or original response to the light or bell stimuli, (*b*) the unconditioned reflex to the electric shock, and (*c*) the CR.

Preconditioning responses to bell and light were generally small reactions, in the sense that they seldom included the whole organism. They were likely to involve an increase in the movement of the pectoral fins, and possibly movements of the eyes in the case of the light. Almost never was there a directional orientation of the body as a whole.

The unconditioned reflex, on the other hand, was a violent flight reaction in the direction of the positive pole of the electrodes. The head would turn toward the positive pole, and the fish would dash toward it, in some instances with such vehemence that it would strike the glass behind the electrodes. Occasionally, if a mullet was crosswise in the tank, or if its tail happened to be pointing in the wrong direction, the force and speed generated in turning might take it entirely out of the water. In every instance, for perhaps 0.1 sec. before the flight-movement began, there was perpendicular erection of the dorsal fin and a rigid stiffening of the pectoral fins, evidently produced by the electric charge.

The conditioned response to both the light and the bell was in a sense opposite to the unconditioned reflex. The fully established CR, which occurred during the 2-sec. portion of the trial when the conditioned bell or light was presented alone, was a gradual lowering of the head end of the organism and a backing away from the positive electrodes. It was a deliberate and slow reaction, yet obviously an avoidance response. This negative orienting movement was usually accompanied by a raising of the dorsal fin as in the case of the unconditioned reflex. In the CR, however, the extension of the fin was never as speedy, as extensive, or as mechanical as it was in the case of the unconditioned reflex.

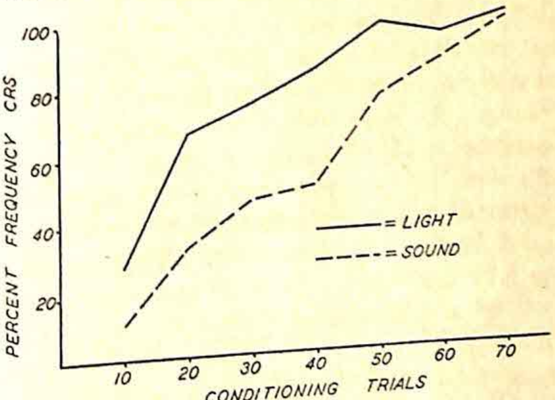

FIG. 1. Curves of the acquisition of the CR for two equivalent groups of salt-water fish

The acquisition of the CR. Learning or conditioning curves, showing the rate of acquisition of the CR, for both the bell (sound) and the light groups, are presented in Figure 1. On the abscissa are given the number of trials in units of 10 trials each, whereas the ordinate shows the percentage of CR's per group, within each unit of 10 trials. Each point on each graph represents the performance of eight fish for 10 trials each, or a total of 80 trials. It is apparent from these curves that the light group conditioned considerably faster than the bell or sound group. The relative speed of conditioning by the two methods is shown by the fact that group L (light) reached the point of 95 per cent efficiency on trial 50 whereas group B (bell) did not reach this level until trial 70.

That an organism as low in the phyletic scale as the striped mullet can develop a CR of this sort in 70 trials or less may at first glance appear to be surprising. It must be remembered, however, that this experiment demonstrates "generalized" rather than "adaptive" or "specific" conditioning. Culler (5) has made clear the distinction between these two levels of learning. In the case of the dog in the buzz-shock conditioning experiment, for example, conditioned struggle to the buzz (generalized conditioning) may appear within from 3 to 15 trials, whereas adaptive conditioning including only the lifting of the reinforced foot may require upwards of 200 trials (12). It has also been shown by Bull (4) that many of the common teleosts will develop CR's in less than 40 trials.

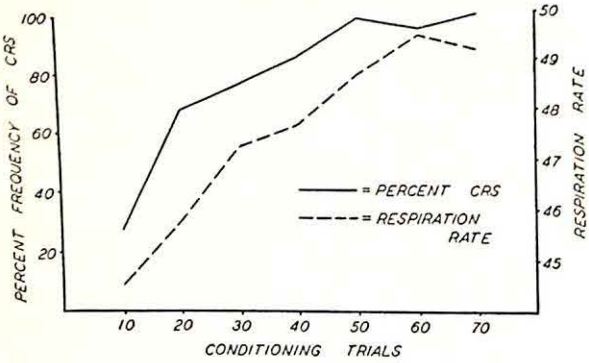

FIG. 2. The relationship between respiration rate and the acquisition of a CR to a visual stimulus in a group of eight striped mullet

The respiration rate and conditioning. The relationship between the average respiration rate of the eight fish in group L (per 15-sec. interval per trial) and the number of conditioning trials is indicated in Figure 2. For comparative purposes, the acquisition curve for group L, which was previously diagrammed in Figure 1, is reproduced again in Figure 2. The vertical scale to the left in Figure 2 applies to CR's, and the vertical scale to the right applies to respiration rates. The similarity between the two graphs is so close that one might almost suppose the respiration graph was also a learning or acquisition curve.

The same sort of relationship (not shown here) existed between the rate of acquisition of the CR in the bell group, and the change in respiration rate as training progressed in that group—with this interesting difference. The respiration rate for group B increased more during the conditioning process than the respiration rate for group L. Rank-difference correlation coefficients between the efficiency of conditioning and respiration rates for the two groups are shown in Table 1.

These high positive correlations between the rate of conditioning and the respiration rate would seem to point to the reinforcing shock as the common factor in both situations. The shock we know to be the reinforcing or motivating agent for the conditioning. The increase in respiration must also be due in large measure to the cumulative effect of many repeated shocks. If one is willing to regard this change in respiration rate as evidence of the building up of an "emotional" or an "anxiety" state, then as the anxiety state builds up, the efficiency of the learning increases. Such reasoning can be fitted rather well into the framework of reinforcement theory in learning.

TABLE 1

Rank-Difference Correlation Coefficients between Efficiency of Conditioning and Respiration Rates

GROUP	CORRELATION COEFFICIENT	LEVEL OF CONFIDENCE
L	.83	.01
B	.71	.05

Extinction. The results obtained from the extinction group (group E) in general support this thesis inasmuch as the respiration rate was found to return to normal as soon as the shock had been removed. With the single exception of fish number 23, which was originally conditioned to light, the extinction rate was so rapid that graphs of the change in respiration during extinction could not readily be drawn. It was possible, however, to record the respiratory change in number 23 throughout a long extinction period of 71 trials which was required before this animal reached the extinction criterion of 10 successive trials with no CR's. The gradual decrease in respiration rate to the normal level throughout these extinction trials is shown in Figure 3.

It should also be noted, so far as the bell and light groups are concerned, that the average rate of extinction for group L (exclusive of fish no. 23) was somewhat slower than it was for group B. In other words, the visual conditioning was in general more resistant to extinction than the audiovibratory conditioning. Here again is further confirmation of the greater effectiveness of the visual situation.

Light, sound, and the respiration rate. If the light and bell (or sound) groups were truly equivalent, as was very likely the case, then the more rapid rate of forming an association with the visual stimulus indicates that the light itself must somehow have had a greater potency or effectiveness for the mullet than the sound stimulus. This may have been due to a relative difference in intensity between the two stimuli so far as the mullet is concerned—the relative intensity being either greater or less for sound than for light. Such a contingency is, of course, impossible to resolve from the present data, although it should be noted that during the preconditioning control trials more responses were made to the light stimulus than to the sound stimulus.

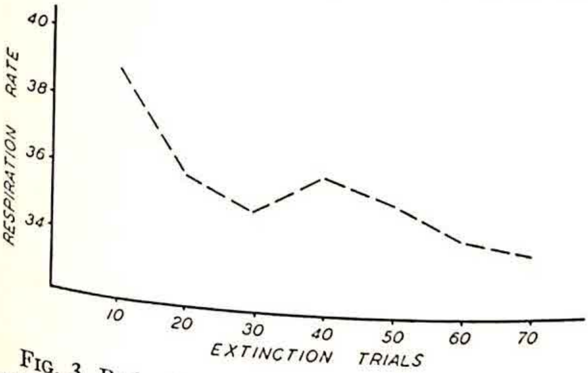

FIG. 3. Reduction in the rate of respiration during extinction. This curve is drawn from the data for one fish only, number 23.

An obvious distinction between the two stimuli lies in the directional nature of the light, which emanated from a particular place or point in space. Because the sounding board constituted the entire back wall of the narrow conditioning compartment, it must have caused all the water in that compartment to vibrate with approximately equal amplitude. The audiovibratory stimulation was consequently nondirectional. Still another difference lies in the nature of the receptors for the two stimuli. Although the receptor for the visual stimulus was obviously the eye, the receptor or receptors for the water vibrations produced by the bell may have been the ear, the skin, the lateral line organs, or any combination of these three.

The various differences in the effectiveness of the light and bell stimuli, as indicated by the performance of the *S*s in this experiment, are summarized in Table 2.

TABLE 2

Contrasting Aspects of the Light and Bell Situations

	LIGHT	BELL
No. preconditioning responses...	greater	less
Rate of conditioning..........	faster	slower
Rate of extinction............	slower	faster
Respiratory increase during conditioning..................	less	greater

SUMMARY AND CONCLUSIONS

Twenty-four striped mullet, *Mugil cephalus*, were conditioned either to a light or to an audiovibratory stimulus, electric shock being used as the unconditioned or reinforcing agent. Extinction was subsequently carried out with four of the animals conditioned in each modality. The respiration rate was systematically recorded after each training or extinction trial for all subjects.

1. In both sorts of conditioning, the conditioned response was qualitatively distinct from the unconditioned reflex. The former was a slow withdrawal *away from* the location of the positive electrodes within the aquarium. The latter was wild orientation *toward* the positive electrodes.

2. Conditioning to the light stimulus was slightly more efficient than conditioning to the sound (bell) stimulus. Conversely, extinction to the light was on the average slower than extinction to the sound.

3. The respiration rate gradually increased during the conditioning training and decreased during extinction. Yet the increase in respiration during the sound or audiovibratory conditioning (which was less efficient) was greater than that during the visual conditioning (which was more efficient).

4. If the rise in respiration rate during the learning is taken as the evidence of the building of an increasingly powerful "anxiety state" in these organisms, it is possible to fit the present results into the general framework of reinforcement theory in learning.

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EXPLORATORY BEHAVIOR AS A FUNCTION OF "SIMILARITY" OF STIMULUS SITUATIONS[1]

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The hypothesis of exploratory drive, developed by the writer (3, 4, 5), states (*a*) that a novel stimulus situation evokes in an organism an exploratory drive which motivates exploratory behavior, and (*b*) that strength of exploratory drive, as measured by amount of exploratory behavior, decreases with time of continuous exposure to a given stimulus situation and recovers during a period of nonexposure. This formulation, which has proved useful in explaining certain cases of behavior variability such as spontaneous alternation, emphasizes the role of external stimulation. The dependence of exploratory behavior upon external stimuli together with certain qualitative observations by the author suggested that a principle analogous to stimulus generalization operates in exploratory behavior. Preliminary investigation appeared to confirm this hypothesis. On each of four consecutive days, nonmotivated (for food or water) rats were permitted to explore two mazes in immediate succession. For one group the second maze was identical with the first; for a second group it differed in type of floor covering and in brightness. The latter group exhibited significantly more exploratory behavior in the second maze.[3]

The present experiment is a more detailed investigation of this phenomenon. It is hypothesized (*a*) that the *decrement* in exploratory behavior produced by exposure to one stimulus situation generalizes to other situations, and (*b*) that the magnitude of the generalized decrement decreases as the similarity of the stimulus situations decreases. Stated differently, as the difference between two consecutive stimulus situations increases, the amount of recovery of exploratory behavior in the second situation also increases. Similarity is varied in the present study by using mazes of three degrees of luminance.

METHOD

Subjects

Thirty-two female rats of the Wistar strain, about 100 days old and experimentally naive, were used as *S*s.

Apparatus

The apparatus consisted of three enclosed mazes, identical except for brightness. One was painted flat black, one flat white, and one an intermediate flat gray, and their mean brightnesses were 0.18, 0.55, and 3.30 ft.-L, respectively. Each maze was constructed in the form of an H. Each arm of the H was 24 in. long, 4 in. wide, and 4 in. high (inside measurements), and was covered with hardware cloth. The mazes were placed close together on the floor of a 10-ft. square enclosure formed by black curtains. Illumination was provided by a single 60-w. bulb suspended 5½ ft. above the center of the floor of the enclosure. This setting provided relatively homogeneous extramaze stimulation. The *E* sat in one corner of the enclosure while observing the maze behavior.

Procedure

Before and during the three days of the experiment all animals were allowed free access to both food and water except during the 10 to 15 min. per day when they were actually in the maze. Four rats were assigned at random to each of eight groups. Each group received a different sequence of maze-exposures. Table 1 shows the experimental design.

On day 1 the animals were permitted to explore one maze freely for 5 min., then, after a 5-min. rest period, were allowed to explore a second maze for 5 min. The first maze was black for 12 rats, gray for 8, and white for 12; the second maze was black for 12 rats, gray for 8, and white for 12. Thus, the effect of maze luminance on amount of exploratory behavior can be determined.

On days 2 and 3 the design is somewhat more complicated. Groups I-A through IV-A were exposed to one maze for 10 min., then to a test maze for 5 min.; Groups I-B through IV-B were exposed to one maze for 5 min., then to a test maze for 10 min. The intermaze interval was about 10 sec. for all animals on both days. Thus, the influence of length of exposure to the first maze upon amount of exploratory behavior in the test mazes can be determined. Also, the change in maze luminance from the first to the test maze was varied systematically, in a counterbalanced order, among the groups. This makes it possible to evaluate the effect of exposure to a maze of each degree of luminance upon

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[1] An abbreviated version of this paper was presented at the EPA meetings in Atlantic City, N.J., in March, 1952.

[2] This research was conducted at Cornell University.

[3] Mr. Louis DiMarco ran the animals in the preliminary investigation.

TABLE 1

Experimental Design

DAY	EXPOSURE TIME	GROUP							
		I-A		II-A		III-A		IV-A	
		a*	b	a	b	a	b	a	b
1	5′	B	W	W	G	B	G	B	W
	5′	W	B	G	W	G	B	W	B
2–3	10′	B	B	W	W	B	B	B	W
	5′	W	W	G	G	G	G	B	W

DAY	EXPOSURE TIME	GROUP							
		I-B		II-B		III-B		IV-B	
		a	b	a	b	a	b	a	b
1	5′	W	B	G	W	G	B	W	B
	5′	B	W	W	G	B	G	B	W
2–3	5′	W	W	G	G	G	G	B	W
	10′	B	B	W	W	B	B	B	W

* Each subgroup (a, b) contains two rats.

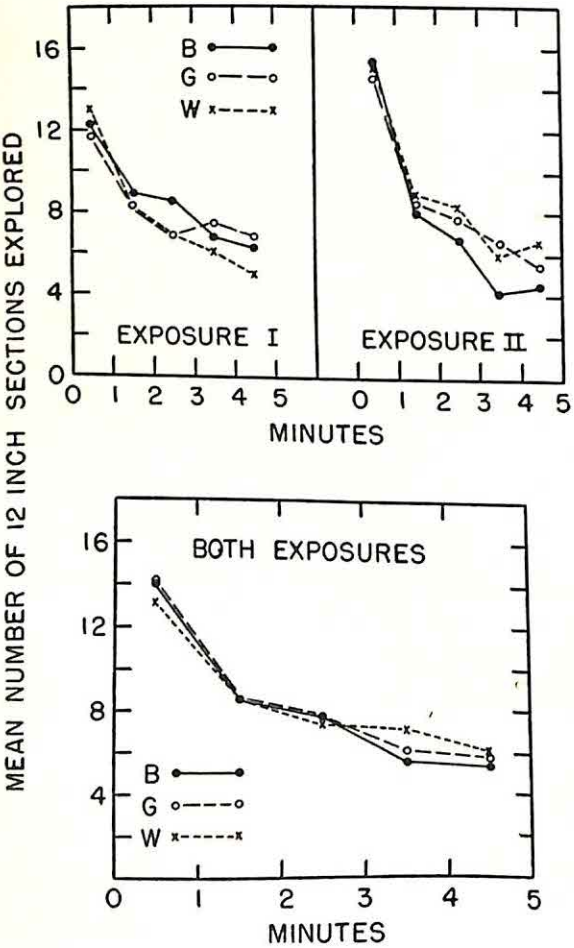

FIG. 1. Mean number of 12-in. sections explored as a function of time of exposure for each maze luminance on day 1

amount of exploratory behavior in test mazes of all three degrees of luminance.

On all days amount of exploratory behavior was measured by recording the total number of 12-in. sections explored during each minute of exposure. The criterion of a maze-section exploration was a full body-length entry, excluding the rat's tail.

RESULTS

The data are analyzed to provide answers to five questions. First, does maze luminance bear any relation to amount of exploratory behavior? Figure 1 shows the average number of 12-in. sections explored plotted against minutes of exposure for the black, gray, and white mazes on day 1. Plots are presented for first exposure, for second exposure (after the 5-min. rest period), and for both exposures. There are no systematic differences attributable to maze luminance. Similar results obtain for days 2 and 3 when the first 5 min. of exposure are considered.

TABLE 2

Mean Number of 12-Inch Sections Explored During the Ten Minutes of Maze Exposure on Day 1

SUBGROUP	GROUP				
	I	II	III	IV	Mean
A	82.2	83.8	75.0	88.0	82.2
B	89.2	82.0	84.0	79.5	83.7
Mean	85.8	82.9	79.5	83.8	83.0

TABLE 3

Mean Per Cent Decrement in Amount of Exploratory Behavior in the Test Maze for Days 2 and 3 Combined

SUBGROUP	GROUP			
	I	II	III	IV
A	−1	31	39	62
B	−3	24	36	59
Mean	−2	27	37	61

Second, are the groups homogeneous with respect to amount of exploratory behavior? Table 2 presents the mean number of 12-in. sections explored by each subgroup during the 10 min. of exploration on day 1. No systematic differences are apparent. Analysis of variance confirms the conclusion that there are no significant differences among groups in amount of exploratory behavior: the F ratio for groups is 0.22, a value that falls short of the .05 confidence level for 7 and 24 *df*.

Third, are there any day-to-day changes in amount of exploratory behavior? The mean number of 12-in. sections explored during the first 5 min. of days 1, 2, and 3 for all 32 rats is 41, 44, and 41. Thus, amount of exploratory behavior is a stable phenomenon over maze luminance, groups, and period of experimentation.

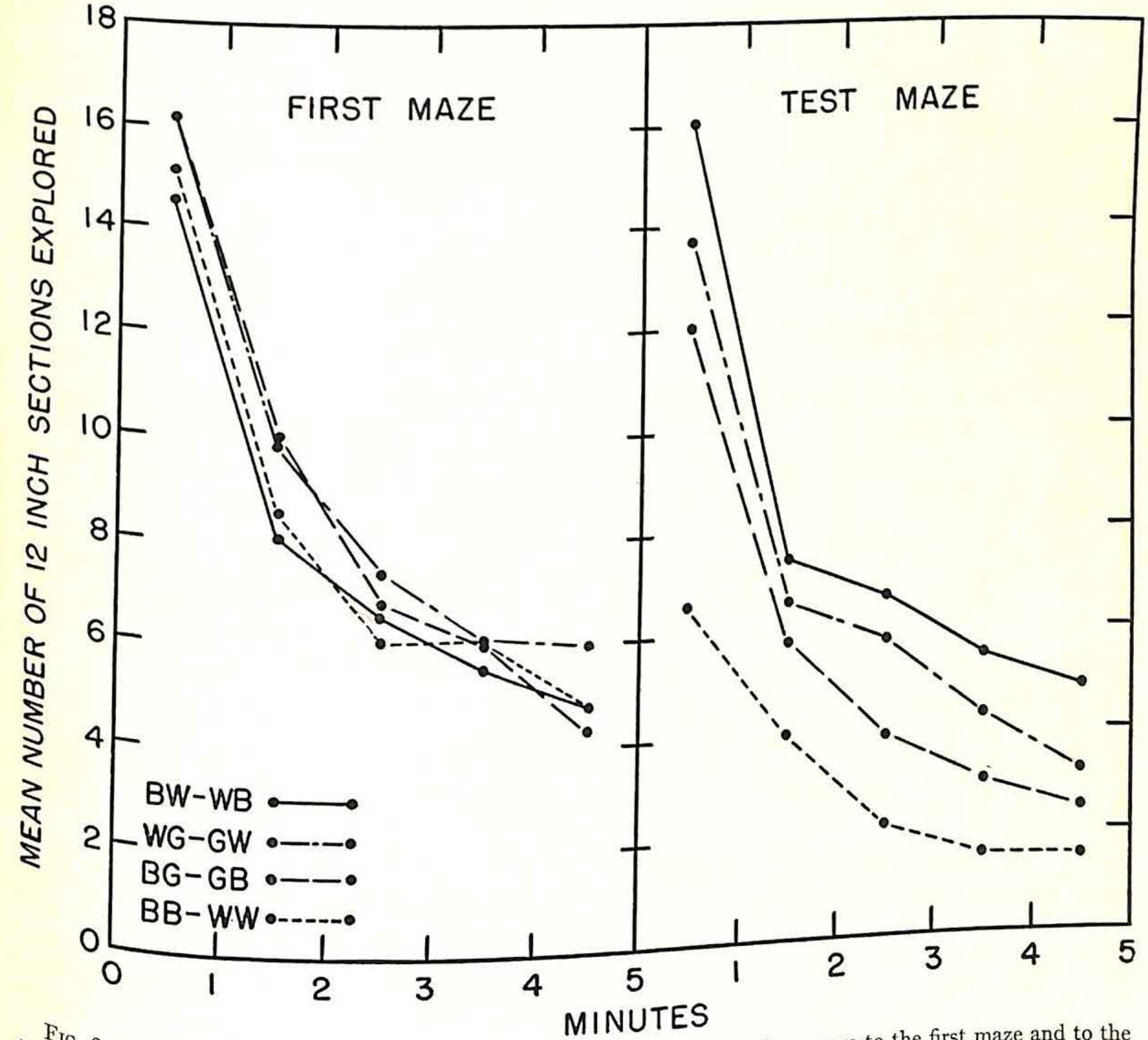

FIG. 2. Mean number of 12-in. sections explored as a function of time of exposure to the first maze and to the test maze for each of the four major groups

Fourth, is amount of exploratory behavior in the test maze a function of the amount of time spent in the first maze (5 min. vs. 10 min.)? Table 3 presents the mean per cent decrement in amount of exploratory behavior during the first 5 min. in the test maze as compared with the first 5 min. in the first maze for the various groups. The data for days 2 and 3 are combined. The A groups (10 min. in first maze and 5 min. in the test maze) show a slight tendency toward a greater decrement than the B groups. However, the results of an analysis of variance show that this tendency is not significant (see below).

The fifth question is the one posed by the experimental hypothesis: Is amount of exploratory behavior in the test maze a function of its difference in luminance from the first maze? Figure 2 summarizes the relevant data.

It shows the mean number of 12-in. sections explored by each of the four major groups plotted against minutes of exposure for the first maze and for the test maze. The data for days 2 and 3 and for the subgroups within each major group are combined. In all cases only the first 5 min. of exposure to each maze is considered. Inspection of Fig. 2 reveals (*a*) that no systematic differences among groups in amount of exploratory behavior occur during exposure to the first maze, and (*b*) that systematic differences do occur in the test maze. The BW-WB group shows the greatest amount of recovery in exploratory behavior in the test maze, the WG-GW group the next greatest amount, the BG-GB group the next greatest amount, and the BB-WW group the least amount. A plot of per cent decrement in exploratory behavior in the test maze against differences in maze luminance in log units yields essentially a straight-line gradient. Thus, amount of exploratory behavior in the test maze is a function of its similarity to the first maze. Reference to Table 3 substantiates this conclusion.

Statistical analysis corroborates this and the preceding conclusion. The per cent decrement in amount of exploratory behavior in the test maze (first 5 min.) as compared with the first maze (first 5 min.) was computed for each rat. These scores were transformed into angles according to the formula, Angle = arc sin $\sqrt{\text{percentage}}$, and were subjected to an analysis of variance. The experimental design permits a two-way factorial analysis, the two components of which are time spent in the first maze (5 vs. 10 min.) and degree of change in maze luminance from the first to the test maze. The F ratio for maze luminance is 43.7, a value significant at well beyond the .001 level for 3 and 24 *df*; the F's for time spent in the first maze and for interaction are 0.65 and 0.21, values which fall short of the .05 level. The greater per cent recovery for the WG-GW group as compared with the BG-GB group is attributable to the fact that the physical difference in maze luminance is greater in the former case.

DISCUSSION

The major finding confirms the experimental hypothesis: The decrement in exploratory behavior produced by exposure to one maze does generalize to other mazes, decreasing in amount as maze similarity decreases. This result is interpreted as providing additional direct support for the hypothesis of exploratory drive. That is, it further emphasizes the importance of external stimulation as a controlling factor in exploratory behavior. It also points to the operation of a stimulus generalization principle in exploratory behavior: When the strength of the exploratory drive evoked by a given stimulus situation is reduced, the strength of the exploratory drive evoked by other similar stimulus situations is also reduced, the amount of reduction decreasing as the similarity of the situations decreases.

There are at least three other theoretical concepts that might be invoked to account for the present results. The first is Hull's (2) construct of reactive inhibition. According to Hull's eighth postulate the performance of a response generates a certain amount of reactive inhibition—a negative drive—which mediates against the repetition of that response and which dissipates with time. This construct could account for the decrement in exploratory behavior produced by continuous exposure to a maze. However, because reactive inhibition is stated to be specific to specific responses, and because the behavior in the first and test mazes involves highly similar if not identical responses, reactive inhibition provides no basis for explaining the differential amounts of recovery of exploratory behavior in the test mazes.

Hull's (2) concept of conditioned inhibition is more promising. Essentially, conditioned inhibition is a habit of resting, i.e., of not-responding, which is conditioned to external stimuli. Hence, it would transfer from one stimulus situation to another in accordance with the principle of stimulus generalization. Although conditioned inhibition could account for the generalization effects from one maze to another that occur on any *one* experimental day in the present study, it leads to the prediction that the decrement in exploratory behavior developed in a maze on any one day would transfer to the next day. Unfortunately for this explanation, exploratory behavior in this and other short-term studies (5) shows relatively complete "spontaneous recovery" over a 24-hr. rest period.

Sometimes exploratory behavior is explained by appealing to a "general activity drive" which supposedly is generated by internal organismic factors. There are at least two reasons why this concept is inadequate as an explanation of the present data. (*a*) It does not account for the rapid decrease in amount of exploratory behavior over short periods of time. In this and previous studies only one-fourth to one-third as much activity occurs during the fifth minute of maze exposure as during the first minute. (*b*) It provides no basis for predicting the differential amounts of recovery of exploratory behavior produced by the variable of maze luminance.

The fact that decrement in exploratory drive and its consequent exploratory behavior generalizes from one stimulus situation to other similar situations makes it possible to account for the gradual decline in exploratory behavior that occurs even in very large mazes. If a maze is relatively homogeneous, then the decrement in exploratory drive produced by exposure to any given segment generalizes to every other segment. The result is a cumulative decrease in the strength of exploratory drive. Thus, it is possible to explain the findings of Dennis and Henneman (1) that rats run in large mazes comprised of homogeneous sections slow down in their activity and often stop exploring entirely. It should not be forgotten, however, that extramaze stimuli play an important role in exploratory behavior, particularly when elevated mazes are employed. Evidence on this point will be presented in a later paper.

SUMMARY AND CONCLUSIONS

Thirty-two albino rats were run in mazes of three degrees of luminance to test the hypothesis that the decrement in exploratory behavior produced by exposure to one stimulus situation generalizes to other similar situations. On the basis of the experimental results and the preceding discussion, the following conclusions are drawn: (*a*) The experimental hypothesis is substantiated: The decrement in exploratory behavior produced by exposure to one stimulus situation generalizes to other situations, decreasing in magnitude as the similarity of the stimulus situations decreases. Hence, a principle analogous to stimulus generalization operates in exploratory behavior. (*b*) Exploratory behavior, of the kind studied in this experiment, is greatly dependent upon stimulation external to the organism. This provides additional support for the hypothesis of exploratory drive. (*c*) The concepts of "reactive inhibition," "conditioned inhibition," and "general activity drive" do not provide adequate bases for explaining the present results.

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SODIUM SUCARYL: A SUBSTANCE WHICH TASTES SWEET TO HUMAN SUBJECTS BUT IS AVOIDED BY RATS[1]

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The affective value of taste stimuli is a little-explored area with important implications for a theory of taste (2). Furthermore, species differences in behavioral measures of taste receptivity may be a strategic point of departure for an analysis of the mechanism of taste. The purpose of this study was to demonstrate a behavioral difference between human *S*s and rats with respect to sodium sucaryl, a nonnutritive substance that is labeled "sweet" by human *S*s.

EXPERIMENT I

The primary purpose of the first experiment was to show that human *S*s increasingly judge sucaryl as sweeter than a standard saccharin solution as the concentration of the sucaryl is increased. A second purpose was to obtain judgments of preference between the standard saccharin solution and the different concentrations of sucaryl.

Method

Subjects and apparatus. The *S*s were 18 Yale students. The apparatus consisted of eight standard medicine bottles and droppers. A screen separated *S* from *E*.

Procedure. Ten paired comparisons between each of seven concentrations of sodium sucaryl (0.33, 0.67, 1.00, 1.33, 1.67, 2.00, and 5.00 gm/100 cc. water) and a standard solution of sodium saccharin (0.13 gm/100 cc. water) were made by each *S*. The presentation of the various concentrations and the sucaryl-saccharin order were completely randomized.

The *S*s were tested about two hours after their evening meal. The *E* placed a drop of the first solution on the center of *S*'s tongue. After *S* rinsed his mouth with water, the second drop was placed and a judgment between the two drops made.

Eight of the *S*s were asked the question, "Which one do you like better?" and ten *S*s were asked, "Which one is sweeter?"

Results and Discussion

Figure 1 shows the percentage of choice of sucaryl over saccharin for the "like" and "sweeter" groups for seven concentrations of sucaryl. The weaker solutions of sucaryl are judged as less sweet than the standard saccharin, but as the concentration increases, the sucaryl is judged as sweeter than the saccharin.

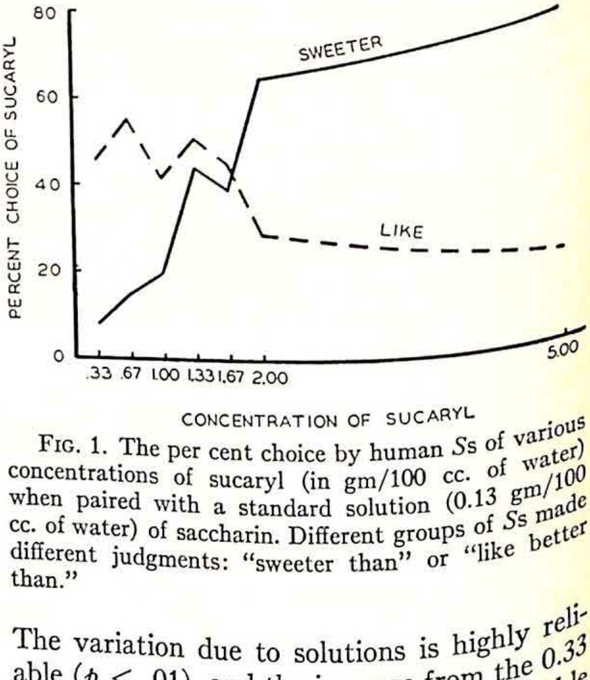

FIG. 1. The per cent choice by human *S*s of various concentrations of sucaryl (in gm/100 cc. of water) when paired with a standard solution (0.13 gm/100 cc. of water) of saccharin. Different groups of *S*s made different judgments: "sweeter than" or "like better than."

The variation due to solutions is highly reliable ($p < .01$), and the increase from the 0.33 to the 5.00 solution is also highly reliable ($p < .001$). Subjects liked the weaker solutions of sucaryl equally as well as the saccharin but preferred the saccharin to stronger solutions of sucaryl. The variation due to solutions is almost reliable ($p < .06$), and the sharpest drop (from solution 1.33 to 5.00) is somewhat reliable ($p < .05$). An analysis of variance shows that the difference in trends between the group judging which they liked better and the group judging sweetness is highly reliable ($p < .01$).

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[1] This study was supported by the Institute of Human Relations, Yale University; Mr. Wells worked as a Bursary Aide. Part of the study was presented at the Connecticut Valley Psychological Association, Storrs, Connecticut, May, 1952. The authors express their appreciation to Dr. Arnold E. Osterberg and the Abbott Laboratories, Chicago, Illinois, for generously donating a supply of pure sodium sucaryl unadulterated by the effervescent compound which is mixed into the commercial tablets.

Since sweetness increases with concentration, the possibility of a complete change in quality from sweet to bitter can be ruled out. The fact that preference decreases to some extent with concentration of sucaryl is at variance with the finding of Engel (1) that reports of "pleasantness" increase as the concentration of sugar increases up to the strongest concentration tested, 40 per cent. This leads us to believe that sodium sucaryl contains an aversive component which increases disproportionately with increasing concentrations of sucaryl. However, an alternative hypothesis is that sugar solutions sweeter than 40 per cent are aversive because of excessive sweetness per se and that the stronger solutions of sucaryl were this sweet. Therefore, in order to conclude that sucaryl contains an aversive component, it is necessary to show that the strongest solution of sucaryl used in this experiment is not sweeter than the 40 per cent solution of sugar which Engel found was "pleasant."

EXPERIMENT II

The purpose of this experiment was to show that the strongest solution of sucaryl used in this study was not sweeter than a 40 per cent solution of sugar. In addition, data were obtained on the presence of taste qualities other than sweetness in sucaryl.

Method

Subjects and apparatus. The *S*s were nine additional Yale students. The apparatus consisted of two standard medicine bottles and droppers.

Procedure. Eight paired comparisons of the sweetness of a 5 gm/100 cc. of water solution of sodium sucaryl and a 40 per cent solution of sucrose were made by each *S*. The order of presentation was randomized. The *S*s rinsed their mouths with water after each stimulus presentation.

The *S*s were also asked to report the presence or absence of the taste qualities of sweet, bitter, sour, and salty in every stimulus presented.

Results and Discussion

The *S*s judged the solution of sugar as sweeter than the solution of sucaryl on an average of 56 per cent of the comparisons. This includes five *S*s who judged the sugar as sweeter, two who judged the sucaryl as sweeter, and two who judged them equal. We can conclude that the strongest solution of sucaryl used in this study is not sweeter than the 40 per cent solution of sugar which Engel's *S*s judged "pleasant." This enables us to say that the decreasing preference of sucaryl as its concentration is increased is not due to reaching any aversive level of sweetness and hence must be due to some different component in the taste of sucaryl.

All *S*s judged all the sugar and sucaryl stimuli as sweet. In the 72 presentations of sucaryl, a salty taste was reported 5 times, a sour 10 times, a bitter 17 times, and an "unspecifiable" taste (which was related to bitter when described) 9 times. The presence of nonsweet qualities was reliably less with sugar as the stimulus ($p < .01$). We conclude that sucaryl contains some nonsweet taste quality.

EXPERIMENT III

The purpose of this experiment was to compare the preference of rats for the standard saccharin solution used in Experiment I with their preference for the three concentrations of sucaryl which human *S*s find about equal to the standard saccharin solution in liking and sweetness. Since exploratory work had shown that rats strongly preferred the saccharin to the sucaryl, the ability of the test to detect any slight liking of sucaryl was increased by comparing saccharin and sucaryl separately with plain water.

Method

Subjects and apparatus. The *S*s were 12 albino rats averaging about 120 days of age and 300 gm in weight. They were housed in a bank of individual cages each of which had two graduated cylinders with precision-made drinking tubes protruding through openings in the rear wall.

Procedure. The procedure duplicated that used by Sheffield and Roby (3). The rats were given two habituation days in the cages while satiated for food and water followed by a day without food. Then for five days the rats were fed 8 gm of ground Purina Chow mixed with 10 cc. of water. Water was available in both cylinders during this time. Following this there were eight days of alternate training and testing. On *training* days a saccharin or sucaryl solution was on a given side for a given animal, and water was on the other side; on alternate *testing* days water was on both sides. The saccharin or sucaryl side was on the left for half of each group and on the right for the other half. Six rats were given the standard saccharin solution (0.13 gm/100 cc. water) on training days. The other six rats were divided into three pairs. Throughout training each pair was given one of the three concentrations of sucaryl (1.00, 1.33, 1.67 gm/100 cc. water) which were judged by humans as about equal in sweetness and preference to the 0.13 saccharin solution. The amount drunk in 24 hr. from each cylinder was measured every day just prior to feeding. The rats were fed 8 gm of ground Purina Lab Chow mixed with 10 cc. of water on each training and testing day.

Results and Discussion

The results for the saccharin and sucaryl groups on the training days are presented in Figure 2. Since the three pairs with different concentrations of sucaryl showed no reliable differences, they are grouped together. The saccharin results are in substantial agreement with those of Sheffield and Roby (3). The per cent choice of saccharin over water is much higher than the per cent choice of sucaryl over water. This difference is extremely reliable ($F = 377$, $p < .001$). The sucaryl choice shows a downward trend on successive days while the saccharin choice is constant throughout. Furthermore, the average amount of saccharin drunk on each training day was 168 cc. as compared with an average of 2 cc. of sucaryl.

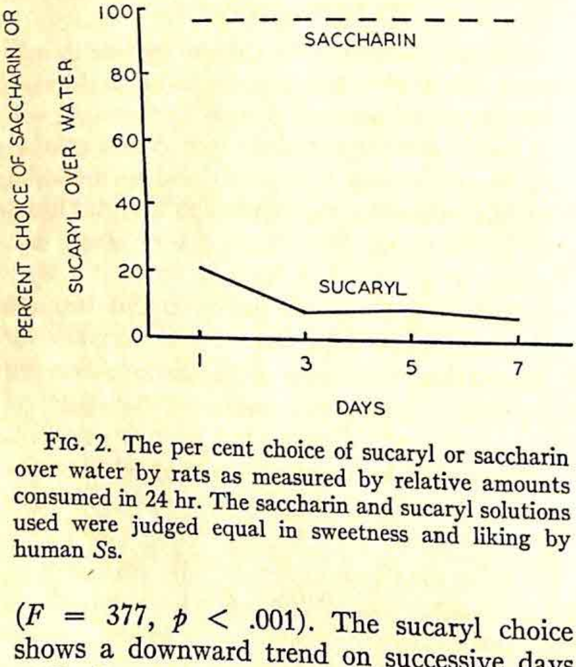

FIG. 2. The per cent choice of sucaryl or saccharin over water by rats as measured by relative amounts consumed in 24 hr. The saccharin and sucaryl solutions used were judged equal in sweetness and liking by human *S*s.

On testing days the per cent choice of the "sucaryl side" over the "water side" decreased consistently but not reliably from 49 per cent on the first day to 14 per cent on the last day. The per cent choice of the "saccharin side" over the "water side" increased reliably ($p < .03$) from 38 per cent on the first day to 61 per cent on the second day and then decreased but not reliably to 33 per cent on the last day. The increase indicates some approach learning with saccharin as opposed to consistent avoidance learning with sucaryl.

We conclude that rats prefer the standard saccharin solution used in Experiment I to water but prefer water to concentrations of sucaryl judged by human *S*s as equal in liking and sweetness to the standard saccharin solution.

EXPERIMENT IV

It was found in Experiment I that human *S*s judge weak and moderate solutions of sucaryl as equally preferred to a standard saccharin solution. The rats in Experiment III preferred the standard saccharin solution to water but chose water over three moderate concentrations of sucaryl. However, the difference in the testing procedures does not permit a simple, direct conclusion about a species difference. The purpose of this experiment was to compare directly the preference of rats and human *S*s for a wide range of concentrations of sodium sucaryl under comparable testing conditions. For both species the choice was between sucaryl and water.

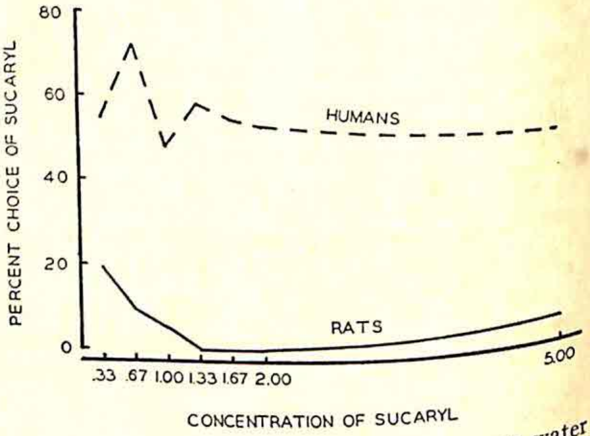

FIG. 3. The per cent choice of sucaryl over water by human *S*s and rats for various concentrations of sucaryl in gm/100 cc. of water

Method

Subjects. Three male, albino rats averaging 140 days old and three male, human *S*s were matched as described below.

Apparatus. The apparatus for the rats was a wooden box 6 in. by 9 in. by 6 in. with a raised hardware cloth floor to prevent the accumulation of drippings. In the metal front of the box there was a 1.5-in. square opening which could be covered with a sliding metal door. Outside the opening a movable rack held three glass cylinders with precision-made glass drinking tubes. Only two of the three tubes were opposite the opening at any one time.

The apparatus for the human *S*s consisted of a set of eight standard medicine bottles and droppers. A screen separated S from E.

Procedure. The rats were deprived of food and water for two days, and then a hunger and thirst rhythm was established for three preliminary days and the seven experimental days by giving the rats access to wet, ground Purina Chow and a water bottle for an hour each day after the testing time.

A trial consisted in 5 sec. of access to a tube of sucaryl and a tube of water. A trial was scored as a sucaryl choice if the rat spent more than half the time at the sucaryl tube; the choice was clear-cut in every case. Position habits were prevented by shifting the rack containing two water tubes and a center sucaryl one every four trials. Trials were massed and terminated after three successive refusals of both tubes.

One of the following seven concentrations was used each day: 0.33, 0.67, 1.00, 1.33, 1.67, 2.00, and 5.00 gm/100 cc. of water. Two rats were tested in an ascending order and one descending.

The procedure for the human *S*s was designed to parallel that of the rats. Testing was done in the late afternoon after a 6-hr. abstinence from food and water.

A trial consisted in placing a drop of sucaryl and then a drop of water on the center of the tongue and asking the subject, "Which one do you like better?" The order of presentation was varied randomly. Each human S was randomly matched with a rat. Each human was given 20 trials a day, but the number of trials and concentration used in the analysis was the same as his rat partner had had for the same day. (Actually, there was little difference in the results when all 20 trials were considered.)

One of the same seven concentrations was used each day. Two *S*s were tested in an ascending order and one in a descending.

Results and Discussion

Figure 3 shows the percentage of the trials on which the human *S*s and the rats chose each of the seven concentrations of sucaryl. The over-all level of the human *S*s is reliably higher than that of the rats ($p < .01$). The human *S*s start out with a slight preference for sucaryl; the rats with a marked aversion. As the concentration of sucaryl increases, the choice of sucaryl by the rats decreases sharply and reliably. The variation due to solutions with the rats is highly reliable ($p < .01$), and the drop from solution 0.33 to solution 1.33 is also reliable ($p < .001$). Similar results were also secured on three additional rats in a preliminary study under slightly different conditions. On the other hand, the human *S*s show an initial rise and then a slight and unreliable drift down in choice of sucaryl as the concentration increases. The variation due to solutions with the human *S*s is not reliable ($p < .10$), and there is no reliable difference between lower and higher solutions. However, a similar downward trend after an initial rise was also found in Experiment I; its reliability may be masked by large individual differences.

SUMMARY AND CONCLUSIONS

Human *S*s judge weak solutions of sodium sucaryl as less sweet than a standard saccharin solution, but as the concentration of the sucaryl is increased, it is judged as increasingly sweeter than the saccharin. The human *S*s like the sucaryl about as well as the saccharin at low and moderate concentrations but prefer the saccharin to high concentrations of sucaryl. Control comparisons with sugar show that this is not due to an aversion for excessive sweetness per se.

Rats prefer the standard saccharin solution to water but prefer water to the three moderate concentrations of sucaryl which the human *S*s like equally as well as the standard saccharin.

Tested in a comparable procedure, human *S*s show a slight preference for sucaryl over water while rats show a marked aversion for the sucaryl. As the concentration of the sucaryl is increased, the rats show a greater aversion.

We conclude that rats and human *S*s differ markedly in their relative preferences for saccharin and sucaryl. This difference indicates that the taste mechanisms of the two species are different. This difference may be related to the thresholds for "sweet" and "bitter" stimulation elicited by sucaryl.

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CONSISTENCY OF SEXUAL BEHAVIOR PATTERNS IN INDIVIDUAL MALE GUINEA PIGS FOLLOWING CASTRATION AND ANDROGEN THERAPY[1]

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The effects of castration and subsequent treatment with androgen on the sexual behavior of several species of male mammals have been described (1, 4, 5, 6, 9, 10, 11, 12, 14), but for the most part these studies have contributed little information bearing on the hypothesis that the pattern of sexual behavior in individual animals is strongly influenced by an inherent reactivity of the tissues mediating this behavior (2, 3, 15). Beach and Holz-Tucker (5) are among the few who related the behavior after gonadectomy and androgen treatment to that prior to the operation. They stressed, however, the effects of different amounts of injected hormone rather than the possible influence of the reactivity of the tissues, although Beach (3) in a review had previously suggested that variation in sexual responsiveness, in addition to being dependent on the amount of hormone, is influenced by the genetically determined reactivity of the nervous mechanisms mediating sexual arousal and mating behavior. Using different methods and the male guinea pig, we have obtained data supporting this suggestion.

METHOD

Two experiments were performed in which sex drive was measured by the method of Young and Grunt (16). When this is done, animals that achieve an average score of 8.50 or higher for 10 tests are considered *high-drive*, those that fall between 8.49 and 6.25, *medium-drive*, and those that receive less than 6.25, *low-drive*.

In the first of the two experiments each of 39 male guinea pigs, 80 to 150 days of age, was isolated. Starting 7 days later, 41 weekly tests of sexual behavior were begun. The first 10 tests were used to determine the score during the precastrational period. Following the tenth test, all but 10 of the animals, the intact controls, were castrated. During the next 16 weeks no therapy was given, and sexual behavior decreased to a constant low level, referred to as the *base line*. Following the twenty-sixth test, which was 17 weeks after castration, 22 of the castrates were given testosterone propionate[3] daily by subcutaneous injection. They received 25 γ per 100 gm. body weight for the first 10 weeks, and 50 γ for the last 5 weeks. The remaining 7 animals were injected with sesame oil and served as the castrate controls.

In the second experiment 31 animals were used. They were divided into four closely matched groups, each having an average score of 7.8 during the precastrational period when the first 10 tests were given. Following castration these animals were tested for the next 16 weeks when no therapy was given. Beginning the twenty-seventh week and for the remaining 15 weeks of the experiment, each group was injected daily with 12.5, 25, 50, or 100 γ testosterone propionate per 100 gm. body weight and given weekly tests. This range of hormonal dosages was used in order to determine the effect of different levels of hormone on the restoration of the sexual behavior characteristic of the precastrational period.

In analyzing the data obtained from the two experiments, it was necessary to make allowance for a feature of the method of scoring which has not hitherto been considered. The score is a composite of the various elements of the behavior pattern: nibbling, nuzzling, mounting, intromission, ejaculation, and the length of the interval between the beginning of the test and ejaculation. It is conceivable that a large amount of behavior of a low order, for example, nuzzling, and a small amount of behavior of a high degree, such as intromission, might give the same score. If so, change in patterns of behavior rather than change in score would be more indicative of the extent to which the behavior restored by hormonal therapy resembles that displayed prior to castration. The data were treated accordingly. Several elements of the sexual behavior pattern were measured and the results plotted as three-point running averages. The elements are the percentage of males achieving at least one ejaculation, the percentage achieving at least one intromission, the percentage mounting at least once during the test period, and the length of the interval from the start of the test to the accomplishment of each of these acts. This latter is called the *latency* period.

The animals used in both experiments were homogeneous as to age, diet, the season of experimentation, methods of handling, and general endocrine balance as judged by the conditions of the individuals at the beginning of the experiment. They were members of a well-stabilized, healthy colony and showed no effects of the operation or the daily injections.

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[2] Submitted in partial fulfillment of requirements for the degree of Doctor of Philosophy at the University of Kansas.

[3] Testosterone propionate was supplied by the courtesy of Ciba Pharmaceutical Products, Inc.

RESULTS

The effects of castration and subsequent androgen treatment as revealed by the scores are of interest to endocrinologists and have been summarized (7). Briefly, castration was followed by a gradual reduction in the strength of sex drive until the base line was reached. Following treatment with testosterone propionate, the behavior of the injected animals returned to the level maintained by the controls. The animals responded to androgen in relation to the drive prior to castration; those that were high-drive returned to the high level, whereas those that were low-drive returned to the low level. It was shown in addition that once the threshold for the response to androgen was reached, which is between 12.5 and 25γ, fourfold differences in hormone dosage did not cause significant differences in the response. The conclusion seemed justified, therefore, that differences from individual to individual seen in this experiment were not attributable to differences in hormonal level.

An observation not previously recorded had to do with the rate of decrease (per cent change) in the strength of sex drive following castration and androgen therapy. When the average of the precastrational scores for each group was taken as 100 per cent and the subsequent change taken as the per cent variation from this level, the scores of the high-, medium-, and low-drive animals decreased at the same rate to approximately the same base line. The difference between the low-drive group and the other two groups during the last weeks of castration without therapy was not significant. Subsequently, with androgen therapy, the scores of the three groups returned to the precastrational level at approximately the same rate.

Changes in the pattern of behavior following castration and androgen therapy are indicated by the data bearing on the percentages of animals ejaculating, achieving intromission, and mounting, and the latency period for ejaculation, intromission, and mounting. Ejaculation was achieved by the intact animals in more than 50 per cent of the tests during the precastrational period (Fig. 1*A*). A rapid decline was seen following castration. Within 2 weeks less than 20 per cent of the castrates ejaculated; within 4 weeks less than 5 per cent; and within 6 weeks less than 2 per cent. By 9 weeks after castration ejaculation was generally eliminated. Occasionally, however, an individual may again become active and display ejaculatory behavior. One male 15 weeks after castration showed intromission accompanied by the indrawing of the flanks characteristic of ejaculation. With the start of androgen therapy, the animals regained their ejaculatory ability. By 2 weeks, approximately 2 per cent of these animals ejaculated; by 4 weeks, 10 per cent; by 6 weeks, 20 per cent; and by 8 weeks, more than 25 per cent. The percentage of animals ejaculating remained at this level until the end of the experiment; and although it was considerably below the precastrational percentage, it was the same as that of the intact controls of the same age. Doubling the amount of hormone after the thirty-sixth test did not increase the percentage ejaculating; in fact, there was a slight decrease. At no time during the period of androgen therapy did the castrate controls ejaculate.

When the castrates given 25γ followed by 50γ testosterone propionate were divided into three groups on the basis of the score prior to castration (Fig. 1*B*), it became obvious that there also existed wide differences in the ability of these animals to ejaculate, and that the differences were closely correlated with the score. Approximately 75 per cent of the high-drive animals, 55 per cent of the medium-drive, and only 5 per cent of the low-drive animals achieved ejaculation. Following castration, these percentages declined rapidly. Within one week the low-drive animals ceased to ejaculate; the medium-drive animals followed suit by the third week; and by the ninth week, with the exception mentioned above, the high-drive animals were no longer achieving ejaculation. With the administration of the same amount of testosterone propionate per 100 gm. body weight, there was soon a redistribution into the same groups which existed prior to castration.

When four different dose levels of androgen were maintained, the same general pattern of response followed (Fig. 1*C*). Provided 25γ or more of testosterone propionate were given, the percentage of animals ejaculating was sim-

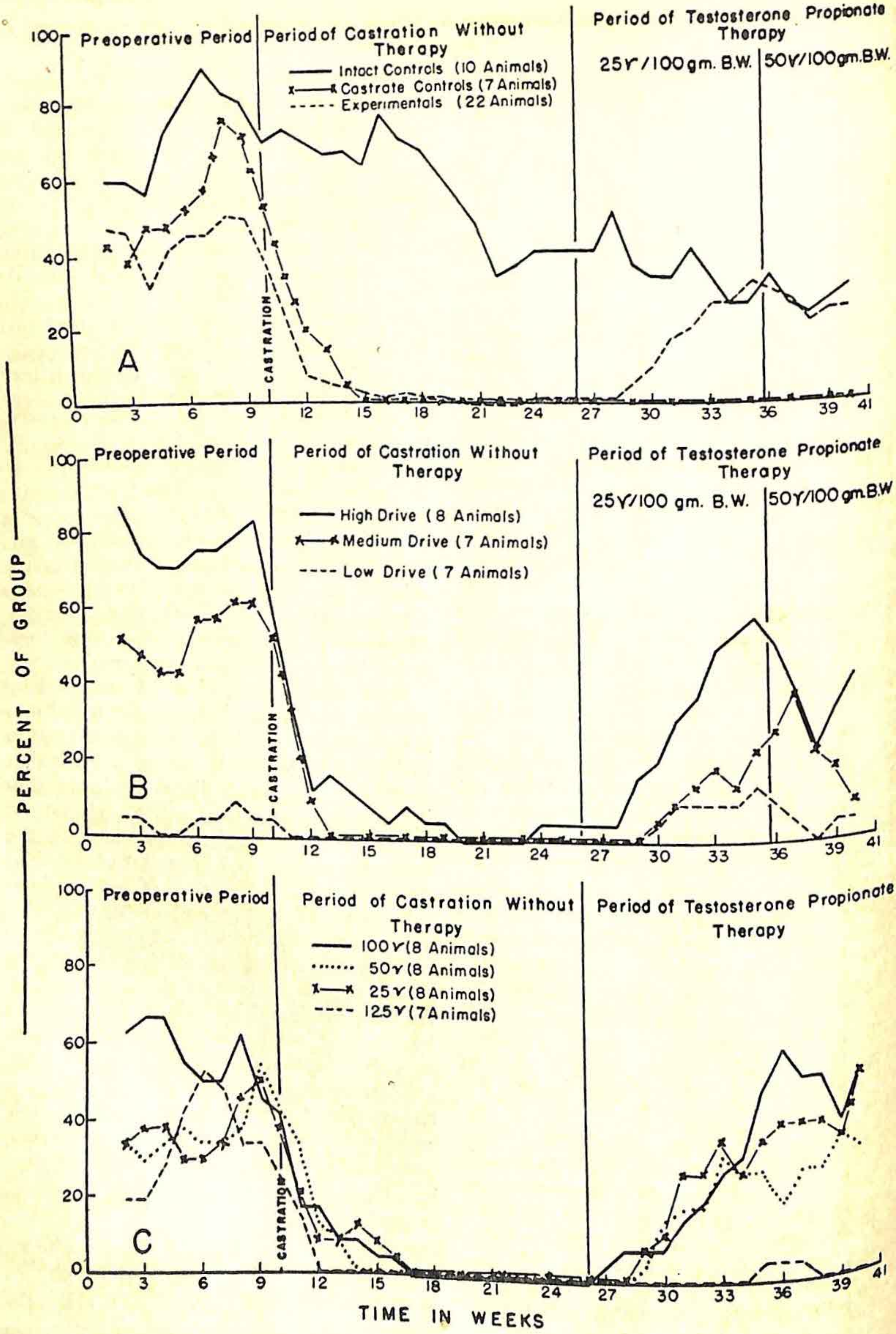

FIG. 1. Percentage of male guinea pigs achieving ejaculation before and after castration and following androgen therapy

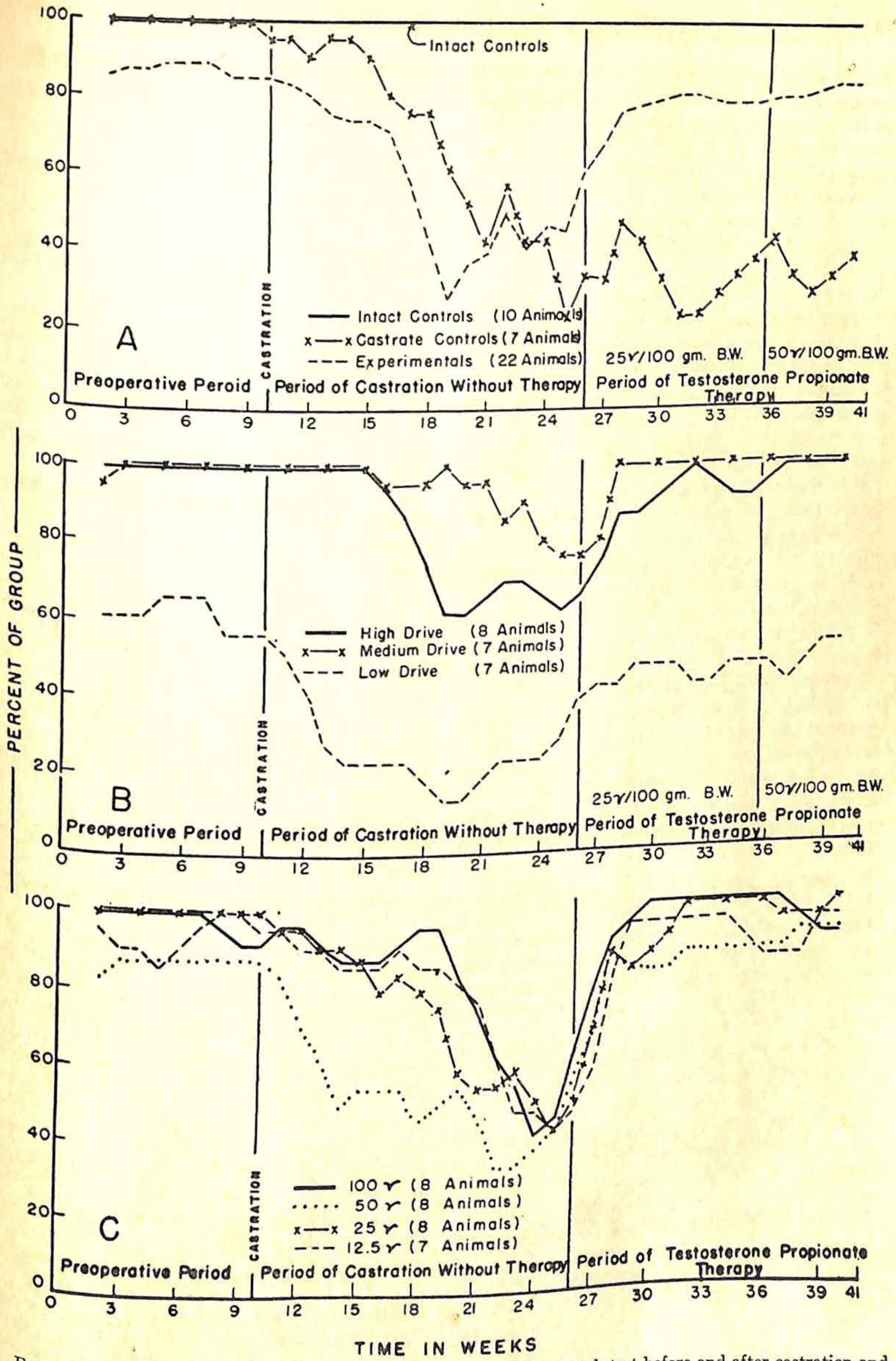

FIG. 2. Percentage of male guinea pigs mounting at least once during each test before and after castration and following androgen therapy

ilar to that prior to castration; a fourfold increase did not affect the result significantly. A dose level of 12.5γ was obviously subthreshold, for in only 2 of 105 tests did animals with this dose level achieve ejaculation.

When the percentage of animals reaching intromission was subjected to analysis, it was found that approximately 85 per cent of the animals displayed this measure of sexual behavior during the precastrational period. Following castration the per cent decreased to 0, but the change was not as abrupt as it was in the case of ejaculation. With therapy the increase in the percentage achieving intromission was rapid, by the second week approximately 15 per cent of the castrates had achieved intromission; and this percentage increased steadily until the ninth week, when more than 55 per cent achieved intromission.

Changes in the percentages of high-, medium-, and low-drive animals achieving intromission were followed. As with ejaculation, the decrease to a base line following castration was rapid. With androgen therapy an increase was shown, the amount depending on the percentages of intromission prior to castration.

The injection of different amounts of androgen gave results similar to those obtained for ejaculation. About 70 per cent of the animals reached intromission whether 25, 50, or 100γ of androgen were given, whereas only approximately 35 per cent of the animals given 12.5γ did so.

Mounting was seen at least once during each test in approximately 95 per cent of those made prior to castration (Fig. 2*A*). Among the intact controls, there was no decrease in this percentage during the 41 weeks of the experiment. Although castration decreased the percentage, the rate of reduction was slow; as long as 31 weeks after castration approximately 35 per cent of the castrate controls were still achieving at least one mounting per test. Treatment with testosterone propionate was followed by a prompt increase in the number of animals mounting; within 2 to 3 weeks the precastrational level was reached.

When high- and medium-drive animals were compared, few differences were seen (Fig. 2*B*). Prior to castration almost all these animals mounted at least once during each test. Six weeks after castration decreases occurred; but with androgen therapy both groups returned to a level near that maintained before castration. The low-drive animals behaved differently. During the precastrational period, approximately 65 per cent of the animals mounted at least once during each test. Following castration this proportion decreased to about 15 per cent; and during the period of androgen therapy about 45 per cent mounted at least once.

Even the smallest amount of injected androgen returned all the castrates to approximately the level seen prior to gonadectomy (Fig. 2*C*). The percentages of animals mounting at least once was about the same whether 12.5 or 100γ testosterone propionate per 100 gm. body weight was injected.

The latency periods for ejaculation, intromission, and mounting constitute a part of the pattern of behavior and were studied accordingly. The results were almost identical with those obtained from analysis of the data bearing on the percentages of animals ejaculating, having at least one intromission, and mounting at least once per test. The latency periods of the groups given therapy were similar to those before castration. For all three measures, 25, 50, or 100γ testosterone propionate restored the latency periods to about the length seen prior to castration. A dose of 12.5γ was completely effective in restoring the latency periods to the precastrational length only for mounting. The supporting data have been summarized graphically, and copies will be supplied on request.

Examination of the data bearing on the percentages of animals achieving at least one ejaculation, at least one intromission, at least one mounting in each test, and the latency periods, reveals that, as with the scores, the response to androgen is strongly influenced by the reactivity of the tissues mediating this behavior. The evidence is perhaps clearest for ejaculation, slightly less so for intromission, and least for mounting, but even in the case of mounting, the sharp separation of the low- and high-drive groups before and after therapy reinforces this conclusion.

DISCUSSION

Of the material presented above, some is new, some is confirmatory of observations made on other species, and some is at variance with results previously reported. In the first category is the validity given the use of the composite score by the results obtained when the separate elements of the behavior pattern are analyzed. Also new is the demonstration that behavior patterns characteristic of the precastrational period tend to be restored in castrate males injected with androgen, and once the threshold is exceeded, there is no significant alteration in the behavior of males receiving fourfold differences in hormone dosage These findings reinforce the hypothesis that differences in sexual behavior of laboratory mammals can be attributed, in part at least, to differences in the reactivity of the tissues mediating that behavior to stimulation by gonadal hormones.

An effect of aging does not seem to have been pointed out. The general decrease in strength of drive in the male has been noted (8), but there is no reference to change in the display of the elements composing the pattern. During the 41 weeks of this experiment, the proportion of animals ejaculating decreased approximately 50 per cent; the proportion of animals achieving at least one intromission per test decreased only about 20 per cent, while the number of animals mounting at least once per test remained constant throughout the experiment.

The data which give confirmation to the results from other species are of interest. Stone (14) and Beach (1) showed that following castration the ejaculatory reflex of the rat is eliminated prior to the copulatory response (intromission). In addition, the action of testosterone propionate restores the copulatory response before the ejaculatory reflex. Comparable data were obtained from the guinea pig. With castration, the order of disappearance of the elements of the sexual behavior pattern is ejaculation, intromission, and mounting; and, as in the rat, the order of return is reversed when androgen therapy is given.

In the rat the different elements of the pattern have different thresholds for androgen (5). Daily injections of 25γ testosterone propionate caused approximately 80 per cent of a group of castrated male rats to achieve copulation, while only 60 per cent achieved ejaculation. Comparable results were obtained when 12.5γ daily of the androgen were injected into the guinea pig. This amount of hormone was scarcely enough to elicit ejaculation, but was sufficient to cause over 35 per cent of the group to achieve intromission and to bring the entire group back to the precastration level of mounting.

Confirmation is given to a suggestion by Stone (13) for the rabbit, that the time interval necessary to drop the copulating drive below the effective minimum for copulation varies directly with the strength of drive at the time of castration. In this work low-drive animals ceased to ejaculate within one week, medium-drive animals by the third week, and high-drive animals by the ninth week. This observation is not inconsistent with the statement that the high-, medium-, and low-drive animals decreased at the same rate. The score is a composite of several elements of the pattern, whereas ejaculation is but one of the elements. More important, the decrease for the high-, medium-, and low-drive males is from a precastrational level taken for comparative purposes as 100 per cent, regardless of the strength of drive.

The data which are at variance with other species require comment. Those obtained from the guinea pig do not support the hypothesis that, within the normal limits of sexual excitability, castration depresses mating tendencies least in the most vigorous copulators and most in the less active individuals (3).

Rats display wide differences in their sexual behavior after castration (4). In contrast, guinea pigs following castration soon showed a very constant low level of sexual activity. Beach and Holz-Tucker (5) state that the administration of 25 to 50γ androgen per day to castrated male rats was followed by a significant increase in sexual behavior. Doses of 75γ testosterone propionate per day or more increased sexual behavior above that seen before castration. In the guinea pig there were indications that increments of androgen up to a point between 12.5 and 25γ per 100 gm. body weight per day increased sexual behavior. On the other hand, once the threshold was reached, as much as 100γ of the androgen per day did not modify the character of the behavior significantly beyond that seen prior to castration.

SUMMARY

The display of elements of the sexual behavior pattern of male guinea pigs, homogeneous as to age, diet, and handling, was tested during the period prior to castration, after castration, and during a period when 12.5, 25, 50, or 100γ testosterone propionate per 100 gm. body weight were injected daily. Differences between individuals were great and permitted a division of the animals into high-, medium-, and low-drive groups. Using the precastrational score as 100 per cent and the subsequent change as the per cent variation from this level, we find the scores of the high-, medium-, and low-drive animals decreased at the same rate to approximately the same base line.

The decrease in the behavior following castration, and the restoration of the precastrational pattern with androgen therapy, were noted. Provided 25γ or more testosterone propionate were given, the pattern was similar to that prior to castration; a fourfold increase did not affect the results significantly. A dose level of 12.5γ was subthreshold for all the elements save mounting. The data support the hypothesis that the behavioral response to gonadal hormones is strongly influenced by the reactivity of the tissues.

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MULTIPLE DISCRIMINATION AND PATTERNED STRING PERFORMANCE OF NORMAL AND TEMPORAL-LOBECTOMIZED MONKEYS[1]

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This report compares the performances of normal and brain-injured animals on two diverse types of visually guided tasks. Such comparisons seem fruitful for indicating the nature as well as the generality of performance decrements which follow cortical assault.

ANIMALS AND OPERATIONS

Two groups of rhesus monkeys served in the experiments. The Normal Group consisted of four intact animals (RF-6, RF-7, RF-8, FT-1) whereas the Temporal Group consisted of four animals that had been subjected to extensive surgical assault to the temporal lobes (RF-1, RF-3, RF-4, RF-5).

All operations were performed in two stages under complete aseptic precautions. Unilateral aspiration of the desired regions occurred in the first stage, and in the second stage, about a week or ten days later, the tissue of the contralateral side was removed in the same manner. In all cases, the surgical approach was by way of the temporal neocortex.

So far as could be ascertained at the time of operation, the greater parts of the hippocampus and the hippocampal gyrus were removed at each operation. The amygdala probably escaped serious encroachment, but exact information must await histological analysis, which is presently being performed. The results of this analysis will be reported in another paper.

The members of the Temporal Group were operated prior to having any formal discrimination training. Before the present experiment was begun, however, both groups were adapted to the test situation and were trained on a series of six discrimination problems scaled in difficulty and involving a total of more than two thousand trials. The animals were thus well tamed and accustomed to routine testing procedures.

MULTIPLE DISCRIMINATION TESTS

Procedure

The animals of both groups were trained to select the rewarded members of a series of 315 pairs of stimulus objects. The members of each pair differed from each other in many respects, and the successive pairs of objects were equally diverse in nature. The two stimuli constituting a problem were presented simultaneously in a duplicate of the Wisconsin General Test Apparatus. With this device the animal confronts a gray tray bearing the two test objects. One member of the pair of stimuli was arbitrarily designated as correct, and its selection resulted in food reward for the animal. The individual test-trial procedures were identical to those used in a number of studies reported by Harlow and his associates (6). A noncorrection procedure was used throughout, and blinds were used appropriately to minimize experimental artifacts.

Each problem was presented for six trials, and six problems were administered each day. The first five problems on any day were completely new to the animals. After the fifth problem, either the first or the fourth problem on that day was reintroduced, but this time the previously unrewarded object covered the food. Thus, each day's testing consisted of five new discrimination problems and subsequently one of these reversed. A total of 315 discrimination and 63 discrimination-reversal problems was presented.

Results

Figure 1 portrays the performances of the Normal and the Temporal Groups on both the new and the old, reversed problems. The graphs show the average intraproblem improvements in performance at three stages of training covering 21 days of testing. The upper panels of the figure apply to the new problems and the lower panels to the old, reversed problems.

All curves show improvement in performance from the first to the sixth trial. The normal animals also show improvement in intraproblem learning from the early to the late stages of training, but no such improvement appears for the operated animals. This difference is most readily seen from the performances on the second trials of the new problems of the two groups at three stages of training. Whereas the trial 2 performance of the Normal Group increases from the first to the last training stage, the comparable score for the Temporal Group does not increase. Identical comparisons for trials 3–6 similarly show interproblem improvement for only the normal animals. Such interproblem improvement has been termed the formation of learning sets (6).

Performance of the Temporal Group on problems presented a second time with reversed reward is depressed only slightly even though these animals attained an average of 75 per cent correct responses on trial 6 when these problems were first presented. Normal animals, on the other hand, continue to select the object rewarded on the initial presentation of the problem, trial 1 performance on the reversed problems being only 25 per cent correct during the first two stages of training. This transfer effect diminishes with further training, and a detailed analysis of the decrement in transfer by the Normal Group has been presented (11). Both groups learned to solve the reversed problems. The Operated Group performed less efficiently on these reversed problems than did the Normal Group during the final stages of training.

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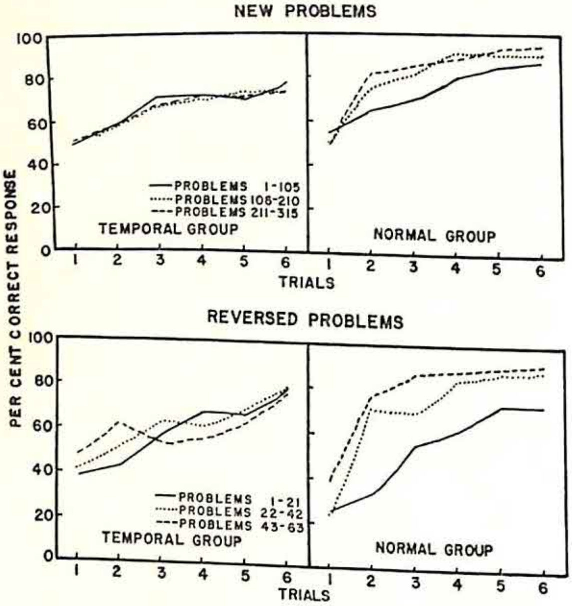

FIG. 1. Intraproblem learning of new and reversed problems at three stages of training by normal and temporal lobectomized monkeys

PATTERNED STRING PROBLEMS

All animals previously described except RF-1 participated in this phase of the experiment. The test requires the ability to trace a chain visually from its attachment to a food morsel to a point within reach of the hand.

Apparatus and Procedure

The apparatus and procedures were similar to those described earlier, the major difference being the use of a large board in place of the tray. At the edge of the board nearest the monkey was located a number of screw-eyes to which the chains could be attached. Six patterns, composed of 2, 3, or 4 chains, were used. The particular patterns were selected from the series used by Harlow and Settlage (7). The rewarded chain varied from trial to trial in a balanced order. The animal was given 25 trials per day on a particular pattern until it reached a criterion of 20 correct responses in one day, or until it had been given 150 trials.

Results

The patterns used and the percentage of correct responses on each pattern for the first day of testing are shown in Figure 2. In contrast to the results of multiple discrimination problems, no systematic deficit can be found for the operated animals on patterned string problems. Although an adequate range of difficulty was covered by these tests, difficulty per se is relatively ineffective for differentiating the normal from the operated animals. Performance of the normal animals was superior to that of the operated animals on only half the problems. These interpretations are borne out by the analysis of variance performed on the data.[2] This analysis revealed that the only significant source of variation was due to an interaction between operation and problem. This is interpreted to mean that there is a tendency for the problems to be ordered dif-

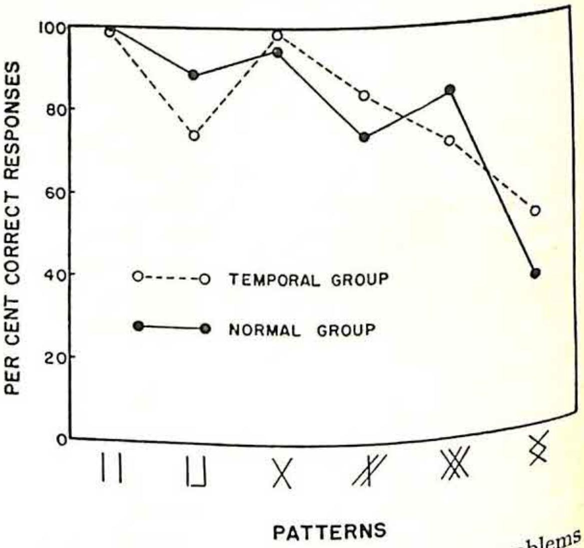

FIG. 2. Performance on patterned string problems by normal and temporal-lobectomized monkeys

ferently with respect to difficulty for the two groups.

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[2] Although detailed statistical analyses are not reported in this paper, they were, nevertheless, performed. Any difference claimed in this report was significant beyond the 1 per cent level of confidence. For detailed statistical analyses and tabular material order Document No. 3907 from the American Documentation Institute, Auxiliary Publications Project, Photoduplication Service, % Library of Congress, Washington 25, D.C., remitting $1.25 for 35-mm. microfilm or $1.25 for 6- by 8-in. photocopies readable without optical aid.

RATE OF PROBLEM ALTERNATION AND RETENTION

The failure of the operated animals to form learning sets despite adequate performance on patterned string problems points to the complex nature of "visual association," and attempts to identify the nature of functional loss following circumscribed insult to the central nervous system will be successful only insofar as they can define the variables underlying performance. Learning sets arise from experience with a large number and wide variety of discrimination problems. Many problems are presented each day with relatively few trials per problem. The failure on the part of the operated animals to form learning sets may stem from the fact that problems are shifted at a rapid rate even though they may be learned if sufficient trials are given in succession. It is conceivable that interferences might arise if problems are alternated rapidly one after another, interferences strong enough to reduce proficiency. The following experiment was performed to check this hypothesis.

Procedure

It was desired to test the effects of rate of alternation rather independently of rate of learning. For that reason four normal and four operated animals (RF-3, RF-4, RF-5, FT-2, unilateral operation) were first given 25 trials in succession on each of ten object-discrimination problems of the type described earlier. After the training series, the animals were tested on these problems for 1, 2, 3, or 6 trials per problem. Every problem appeared six times on each day, the only variation being in the number of times that a particular problem appeared on successive trials. Sixty trials per day were administered for eight days, each rate of alternation occurring on two successive days. The order in which the rates were given varied from animal to animal according to a four-by-four latin square. Two identical latin squares, one for each group, were used so that the variation in performance due to differing rates of problem alternation could be isolated from the effects of differing over-all levels of performance. For each latin square three main sources of variation can be analyzed in addition to experimental errors: *Sequence*, *Order Confounded with Animals*, and *Rates*. The individual test-trial procedures were identical to those described above.

Results

The result of principal interest is that relating proficiency of performance to the number of successive trials occurring in a single problem presentation. Inspection of Table 1 reveals that the number of times a particular problem is presented before going on to the next problem is not a significant factor in determining performance either for the normal animals or for the operated animals. For neither group did the variance due to rate of problem alternation attain the usually required levels of significance.

The two significant sources of variation were *Sequence* and *Order-Animals*. Significant differences between individual animals are to be expected but are of little theoretical interest. The effects of *Sequence* are shown in Table 2. From this table it is seen that successively fewer errors were made on each succeeding pair of test days. In other words, performance continued to improve throughout the eight test days.

TABLE 1

Total Errors per 120 Trials As a Function of Trials per Problem

GROUP	1 TRIAL	2 TRIALS	3 TRIALS	6 TRIALS	SUM
Temporal	27	31	13	26	97
Normal	9	7	8	9	33

TABLE 2

Total Errors per 120 Trials As a Function of Consecutive Two-Day Test Periods

GROUP	PERIOD			
	First	Second	Third	Fourth
Temporal	53	18	16	10
Normal	18	6	4	5

DISCUSSION

The present results indicate that temporal-lobectomized monkeys failed to learn how to learn discrimination problems, but their performance on patterned string problems was generally as efficient as that of normal animals. Thus two diverse samples of visually guided tasks were presented, but the operated animals showed loss only on one of these. The fact that the operated animals exhibited intra-problem improvement suggests that the operated animals gain from specific experience but do not benefit from the broad experience with a variety of problems that is significant for the formation of learning sets.

Decrement in performance on patterned string problems has been shown for a variety of cortical lesions. Temporary loss was obtained by Settlage (12) in animals subjected to bilateral invasion of the occipital lobes. Corresponding loss was found by Harlow (5) in unilateral occipital-lobectomized animals. The dependence of initial postoperative performance upon the degree of intactness of the visual field is further reported in a joint publication by these authors (8). Their partially hemidecorticate monkeys showed more profound loss than was shown by monkeys subjected to bilateral invasion of the frontal regions.

Decrement in performance in such tests by temporal-lobectomized animals has been described by Klüver and Bucy (9, 10). They point out, however, that their animals responded indiscriminately to the strings, and probably did so irrespective of the particular string patterns. The animals of this experiment did not display this compulsive behavior and their proficient performances reflect responses to a well-differentiated field.

The extent to which the failure to form discrimination learning sets is specific to injury to the temporal lobes is, of course, impossible to say in advance of additional experimentation. Data are available, however, which indicate that monkeys subjected to partial hemidecortication can form effective learning sets, and do so at a rate comparable to that of normal animals, although the general level of performance is lower (6). Furthermore, these same animals form pattern-discrimination learning sets even after additional surgical removals of frontal and posterior association areas on the contralateral sides (13).

An increasing number of studies (1, 3, 4) as well as other unpublished data from this laboratory point to the importance of the integrity of the temporal lobes for certain visually guided tasks despite the physiological remoteness of these regions from the primary visual projection area (2). All these studies show differential rather than uniform loss and point to the multivariate nature of visual performance.

SUMMARY

1. The performance of normal monkeys on visually guided tasks was compared with that of temporal-lobectomized monkeys. The operated animals were able to learn specific discrimination problems but were unable to learn them rapidly even after 200 to 300 such problems. The normal monkeys progressively improved in the ability to solve such problems. The operated animals thus failed to form learning sets.

3. There was no evidence of a general loss in the ability to solve patterned string problems by the Temporal Group.

3. A further investigation designed to evaluate the extent to which rate of problem presentation affected performance on multiple discrimination problems revealed that temporal-lobectomized animals, like normal animals, performed as well if problems were changed after every trial as after six trials, at least if both groups of animals had 25 trials' preliminary training on each problem.

4. It was concluded that these animals were unable to benefit from extensive past experience, experience which is only indirectly related to problems engaging their activity.

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THE INFLUENCE OF BEHAVIORAL FACTORS ON THE INCIDENCE OF AUDIOGENIC SEIZURES IN RATS[1]

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In 1942 Lindsley, Finger, and Henry (3) reported that rats, ordinarily susceptible to epileptoid reactions when stimulated with high-frequency sound, failed to have the seizures or to evidence EEG and EKG patterns characteristic of the fits when they were lightly bound and held close to the source of stimulation. At that time the present author (2) found that allowing susceptible animals to make a response just at the point of seizure onset resulted in a failure of the fit pattern to appear. Subsequently, Marcuse and Moore (4), in the course of studying the heart rates of rats during the comatose stage of audiogenic seizures, made the following comment: ". . . it appeared to the experimenter that the rat's attempts to bite the electrodes and his frequent tangling in the wires restricted the frequency of the seizures" (p. 518).

The present observations were made on 40 domesticated Norway rats in connection with a study of EEG and EKG patterns obtained during sound-induced convulsions. All the animals were known to have audiogenic fits more than 50 per cent of the times tested when exposed on alternate days, for a period of one month, to 2 min. of stimulation with a 110-v. electric bell.

METHOD

A Garceau two-channel electroencephalograph was used to obtain brain and heart records from animal *S*s during audiogenic seizures. Small silver disc skin electrodes were fixed with collodion over the frontal and occipital regions of the shaved skull. Similar electrodes were placed on the thoracic cage. The EEG and EKG records were taken in an electrically shielded sound-proofed room according to the following procedures:

Procedure A

Ten rats were confined in a modified Carmichael sock (1) while brain and heart electrodes were fixed in position. This device consisted of a funnel 12 in. long constructed of coat-hanger wires. The narrow end of the funnel was formed by bending the wires into hooks which were fitted into a rubber-lined brass ring 1¼ in. in diameter. At the open, wide end of the funnel the wires were bent into hooks which were pulled through the upper part of an athletic sock. The coat-hanger wires were kept in the shape of a funnel through interlaced thongs; sufficient "give" was allowed to enable electrode placement while the animal was confined in the sock. The animals were run into the sock, their teeth "looped" over the rubber-lined brass ring, and the sock opening squeezed shut behind them. The coat-hanger wires over head and thorax region were forced apart and electrodes placed over brain and heart regions. The subjects were then placed individually on a wooden frame 13 in. by 17 in., the bottom of which was composed of hardware cloth. A circular lid, 12½ in. in diameter, constructed of fiber board and hardware cloth was placed over the animal. The electrode leads from heart and brain areas were passed through the hardware cloth and their jacks connected with the junction box of the electroencephalograph. A heavy-duty electric bell activated by 110 v. was hung 8 to 10 in. over the stimulus chamber and served as the source of auditory stimulation in testing the rats for sound-induced convulsions.

Procedure B

Ten animals were subjected to treatment similar to that described above with one exception. In place of confinement in the sock during the electrode placement, they were given a familiarization period during which time they were handled, stroked, brought into contact with the electrodes, etc., until they tolerated placement of the electrodes while being held by the experimenter.

Procedure C

Ten rats, restrained in the sock during electrode fixing, were placed for auditory stimulation in a sound-proofed pine box, 20 in. by 20 in. by 14 in., equipped with a glass top for observation purposes. The electric bell was fixed inside the box 8 to 10 in. overhead. Electrode leads were passed through holes in the side of the stimulus chamber and connected with the junction box of the electroencephalograph.

Procedure D

Ten animals were subjected to procedure C with the exception of being given an electrode familiarization period in place of the sock confinement prior to bell stimulation in the pine box.

Each rat used as an *S* in the foregoing procedures was exposed to bell stimulation for 2-min. periods on alternate days for a month while attempts were made to obtain brain and heart records during quiescent and seizure states. In taking EEG and EKG records, no attempt was made to record during the violent running attack which preceded the seizures.

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[1] Supported by a Grant-in-Aid from the Division of Research Grants and Fellowships of the United States Public Health Service.

RESULTS

When the animals were subjected to procedure A, they showed neither the audiogenic seizures nor the rather characteristic EEG and EKG patterns which accompany them. The upper portion of Figure 1 shows the brain discharges, the lower portion the heart discharges, recorded following a 2-min. stimulation period with the electric bell. The frequency of the brain discharges ranged from 4 to 7 per sec., that of the heart ranged from 6 to 7 per sec. The responses of the *S*s were marked by violent clawing at the head and heart electrodes, shaking, biting, and scratching at the leads and areas where the electrodes were fixed. These responses seemed to be enhanced in number and tempo when auditory stimulation was given.

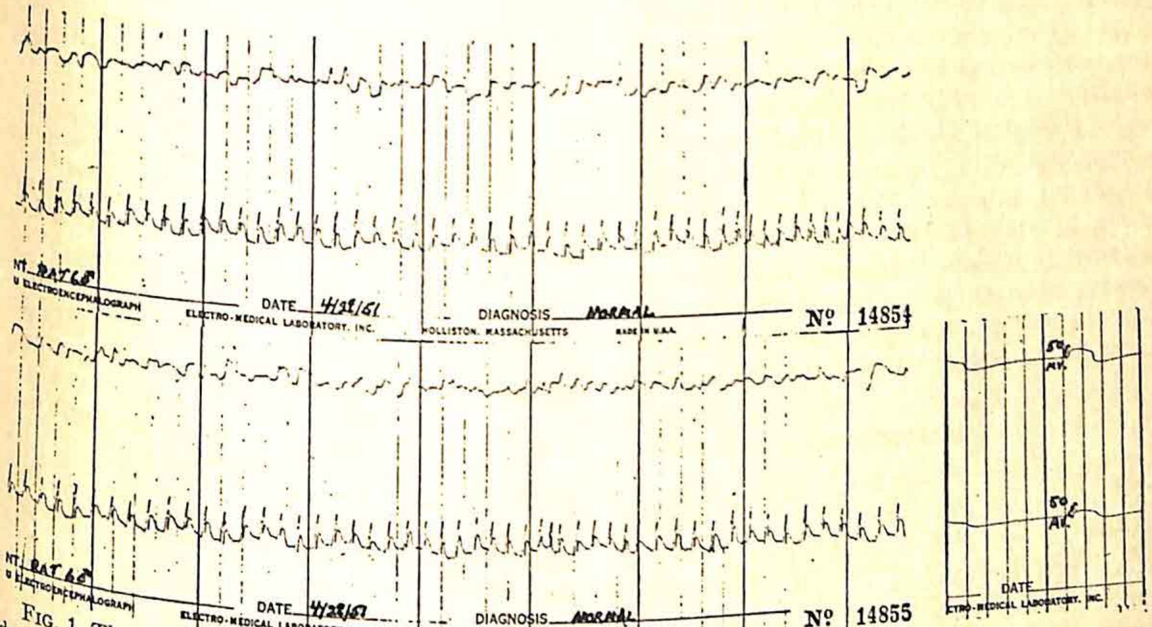

FIG. 1. The above tracings show sixteen seconds of electroencephalogram and electrocardiogram taken on a rat during auditory stimulation. The animal did not experience an audiogenic seizure. The figure at the right is a photo of the normal signals.

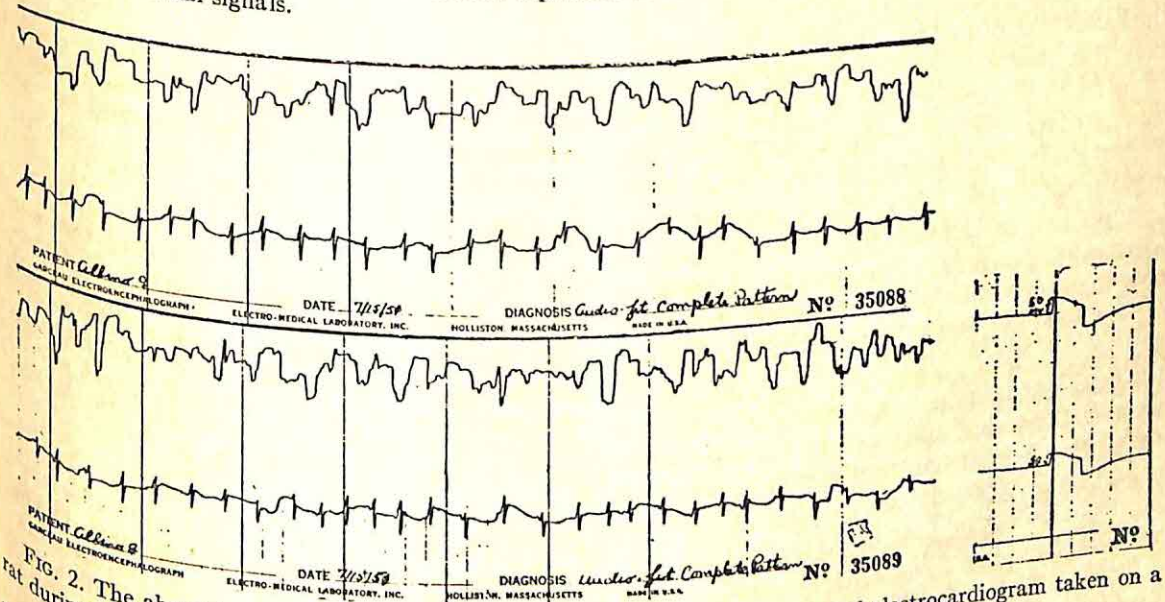

FIG. 2. The above tracings show eighteen seconds of electroencephalogram and electrocardiogram taken on a rat during an audiogenic seizure. The figure at the right is a photo of the fit signals.

In contrast to the foregoing results, all the rats used in procedure B showed typical audiogenic fits. Figure 2 shows a portion of the electroencephalogram and the electrocardiogram taken during the audiogenic seizure. The frequency values for the brain discharges, seen on the upper portions of the tracings, ranged from 2 to 4 per sec., while those for the heart, seen on the lower portions of the records, ranged from 3 to 4 per sec.

Three of the ten animals subjected to procedure C showed complete-pattern audiogenic seizures (2) in excess of 50 per cent of the times tested. Two animals showed fits sporadically (less than 50 per cent of the times tested), and five rats failed to show the seizures during any of the tests. The EEG and EKG records of animals showing the fits resembled, in general, Figure 2, whereas those taken on animals failing to show the fits resembled Figure 1.

Use of procedure D resulted in all subjects showing complete-pattern audiogenic convulsions. The electroencephalograms and electrocardiograms were characteristic of the seizure state.

DISCUSSION

It would appear from the foregoing observations that a central factor influencing the incidence of convulsions in response to sound stimulation is whether or not the animal's environment permits it to engage in manipulative behavior during the stimulation. In no case did the convulsions occur when the *S*s were "working" on the electrode leads during the bell stimulation. Our observations indicated that the hardware cloth chamber was better adapted to the manipulation of the electrode leads, plates, and attachment areas, on the part of the *S*s during auditory stimulation than was the wooden bell box. The latter chamber, because of the location of the holes through which the electrode leads ran to the junction box, made it difficult for the animal to bite or otherwise manipulate the electronic equipment and still remain on its feet. Likewise, less of the electrode leads were exposed when the rats were in the pine box than was the case when they were stimulated in the hardware cloth chamber. It was particularly noted that those animals failing to show the fits when stimulated with the bell in the pine box succeeded in maintaining a stance enabling a degree of freedom for biting, pulling, and otherwise manipulating the electrodes and their leads.

It would seen a reasonable hypothesis that allowing the *S*s to acclimate to the electrodes resulted in a reduction of the manipulative behavior described above, which in turn was related to an increase in the incidence of audiogenic convulsions.

Further study regarding the optimum environment for incidence of sound-induced convulsions in relation to opportunity for behavior or response is indicated. It may be, for instance, that the general failure of the conflict method in the experimental production of convulsions in rats (2) is due to the fact that the method allows the animals to make responses continually even though the responses themselves may be inadequate for problem solution.

SUMMARY AND CONCLUSIONS

Several reports (2, 3, 4), in the literature on audiogenic seizures in rats have mentioned, in an incidental manner, that susceptibility seemed to be affected by the degree to which an animal's environment permitted extraneous and/or manipulative behavior during stimulation.

In connection with the study of brain and heart discharges during sound-induced convulsions, we observed in 40 *S*s of known susceptibility to audiogenic seizures considerable variation in seizure incidence attending different procedures for EEG and EKG recordings when two differently structured stimulus chambers were used.

The hypothesis was suggested that incidence of seizure susceptibility was dependent to a degree on the amount of manipulative behavior in the form of biting, scratching, and pulling at electrodes and leads permitted by the manner in which the stimulus chamber was constructed.

It was further suggested that acclimating the subjects to use of the electronic equipment cut down the amount of manipulative behavior displayed during the auditory stimulation and resulted in an increase in the incidence of audiogenic seizures.

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THE EFFECT OF ELECTROCONVULSIVE SHOCK ON FOOD INTAKE AND HUNGER DRIVE IN THE RAT[1]

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Many studies have used food-motivated maze running to assess the effects of electroconvulsive shock (ECS) on learning and retention. These studies have generally assumed that an impaired maze performance results only from the effects of the shocks on the cerebral functions subserving learning and retention. However, if hunger drive is decreased as a result of shock, an impairment in performance may occur independently of the cerebral effects. That hunger drive may indeed be affected is suggested in the studies of Bernberg (1) and Jensen and Stainbrook (6), who report alterations in the eating behavior of the rat following a series of ECS's. Neither of these studies, however, was designed specifically for the purpose of investigating the effect of ECS on hunger drive.

The study reported here did so, two chief considerations determining the experimental plan. First, since Miller, Bailey, and Stevenson (8) had demonstrated that in rats with lesions in the hypothalamus increased food intake is associated with decreased hunger drive, and since Hoyt and Rosvold (5) had implicated the hypothalamus in the effects of ECS, it was necessary to measure separately the effects of ECS on food intake and hunger drive. Second, ECS in the rat results in decreased activity which may affect eating in two ways: an inactive animal requires less food; the activity of consuming food may be subject to the same reduction as is spontaneous locomotion. Therefore, activity measures were made coincident with the measures of eating behavior.

METHOD

Animals

Twenty-two 160-day-old male albino rats of the Sprague-Dawley strain were housed individually either in separate cages or in activity wheels. They were weighed and then fed at the same time each morning on dry powdered Purina Laboratory Chow from containers designed to eliminate waste. Water was always available. They were placed at random into one of two main groups, one of which was allowed to feed ad libitum and the other of which was kept at 85 per cent of weight. Six animals in each group were shocked; five in each group were maintained as controls.

Shock Procedure

Electroconvulsive shocks were administered one each day for ten days. The shocking apparatus was that used by Rosvold (9) and delivered 50 ma. for 0.2 sec. through alligator clip electrodes attached to the ears, the clips being soaked in sodium bicarbonate solution before use. This equipment invariably produced a generalized convulsion of the type described as tonic-clonic.

Measure of Food Intake

The animals in the ad lib. group ($N = 11$) were allowed to feed ad libitum throughout the experiment, food intake being measured daily. Daily body weights were used as an additional measure of food intake since in the adult white rat measures of body weight tend to be more stable than those of daily food intake.

Measure of Hunger Drive

Bar pressing was used as a measure of hunger drive since it yields a fairly stable measure of hunger and is not likely to reflect any enfeeblement of the animals that may be consequent upon the shock treatment. However, it requires that for effective performance the animal be food deprived. Accordingly the animals ($N = 11$) of this group were kept at 85 ± 2 per cent of weight by adjusting amount of food. These deprived animals were trained under conditions of partial reinforcement to press a bar, and after preliminary training, were run in the bar-pressing apparatus three times weekly, ½ hr. before daily feeding. The apparatus consisted of four bar-pressing cages in which the animals were tested for 20 min. and was so designed that the animals could, by pressing the bar, get food every 3 min. in the form of a pellet weighing about 0.04 gm. The number of times the bar was pressed was counted automatically. The animals in the four cages got their pellets 45 sec. apart, and the order in which the cages had pellets delivered to them was different from session to session.

Measure of Activity

The way in which eating may be affected by changes in activity was specified above. This requires that measures of activity be obtained on the food-intake group. It is clear, however, that the rate of bar pressing also may be affected by such changes. Thus, activity was measured in both the food-intake and the hunger-drive groups. Dashiell-type wheels with drums 14 in. in diameter and tracks 4½ in. wide were used. An attached cage 5 in. by 6 in. by 10 in. enabled the rat to leave the wheel at any time. Since only 16 activity wheels were available, the animals were rotated through the cages so that each animal was in one of two activity wheels two days out of every three.

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[1] This study was supported by a grant from the Veterans Administration, No. VAm 23379.

[2] The authors are indebted to Dr. Neal E. Miller for providing facilities for this experiment and advice on questions of design.

After two weeks of adaptation to this rotation scheme, measures of food intake, body weight, and activity were made for ten days prior to shock. In addition, five bar-pressing tests were made on the 85 per cent of weight animals. These measures served as a base line against which were evaluated postshock variations. During the shock period and for 23 days postshock these same measures were obtained daily for all animals. In addition, bar-pressing tests were given to the 85 per cent of weight group three times weekly for a total of ten postshock measures.

Measure of Food Intake in Hunger Drive Group

Because the results showed opposite trends in the two experimental groups, i.e., increased hunger but decreased food intake, the hunger-drive animals were taken off the restricted diet after ten bar-pressing measures postshock had been obtained and allowed to feed ad libitum for seven days. The amounts of food eaten daily were measured. This procedure permitted, on the one hand, a comparison between measures of eating and hunger drive in the same group, and on the other hand, a comparison between measures of eating in the two groups. It was predicted that the ad lib. feeding of these deprived animals would reflect the same trend as the bar-pressing tests.

TABLE 1

Experimental Design

GROUP	*N*	SHOCK	BAR PRESSING	85% OF WT.	AD LIB. FEED.	ACTIV.	ADDIT. AD LIB.
Hung. drive shock	5	X*	X	X		X	X
Hung. drive control	6		X	X		X	X
Food intake shock	5	X			X	X	
Food intake control	6				X	X	
Total	22						

* X signifies the presence of a particular treatment for a group.

The experimental design is summarized in Table 1.

RESULTS

Food Intake

Table 2 shows the average total food intake of the ad lib. animals in relation to the schedule of shocks. It is clear that electroconvulsive shock *decreases* food intake in the ten days immediately after the series of shocks. This same trend is reflected in the body-weight differences illustrated in Figure 1.[3] The loss in body weight of the shocked animals was never completely recovered during the remainder of the experiment. For the 23-day postshock period as a whole, there is no significant effect on body weight or food intake although there is usually a small difference in favor of the controls. The finding that ECS's in these animals fed ad libitum has the effect of decreasing food intake and body weight corroborates a preliminary finding of the authors in a study in which the rats were fed for 1 hr., sufficient time to permit them to maintain weight, and deprived 24 hr. before bar-pressing tests. In this preliminary study the shocked animals pressed the bar *less* than the controls following shock.

TABLE 2

Average Total Food Consumption Food Intake Groups Before and After Shock

	10 DAYS PRESHOCK	DAYS 1–10 POSTSHOCK	DAYS 11–23 POSTSHOCK	TOTAL DAYS 1–23 POSTSHOCK
Food intake shock	215.2 gm.	206.8 gm.	318.7 gm.	525.5 gm.
Food intake control	212.0 gm.	242.7 gm.	310.8 gm.	553.5 gm.
t	.300	2.54	.670	1.47
p	>.70	<.05	>.50	<.20

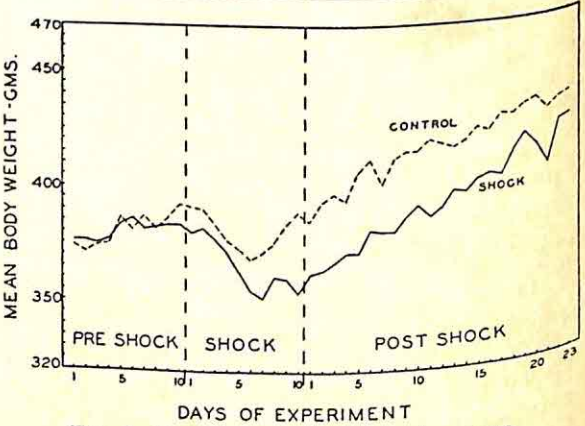

FIG. 1. Body weight of food intake group

Hunger Drive

The bar-pressing curves in Figure 2 demonstrate that the effect of shock is to *increase* sharply motivation for food in the deprived animals as measured by this instrumental response.

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[3] The difference during the shock period is somewhat obscured because an infestation necessitated animals being dipped in oil, on the second day of shock. This had the effect of reducing food intake and body weight in both groups. Nevertheless, that shock does produce a decrement in weight is evidenced by the fact that the greatest loss in weight incurred by the controls is approximately 20 gm., and they returned to their pre-oil dipping weight after 8 days whereas the shock group lost as much as 40 gm. and did not recover its preshock weight until 19 days after the onset of shock.

The t of the difference between the averages of the last five measures postshock approaches significance ($t = 1.95$, $p < .10$). However, when the original scores are taken into account by means of a t of the difference between the preshock-postshock differences (calculated on the basis of five tests preshock and the last five tests postshock), the shock group is significantly superior to the controls ($t = 3.24$, $p < .02$).

At the time the bar-pressing measures were terminated, there was no indication that the high level of bar pressing in the shock group was leveling off. In contrast to the shock group, the control group exhibited a fairly stable level of bar-pressing performance throughout the course of the experiment.

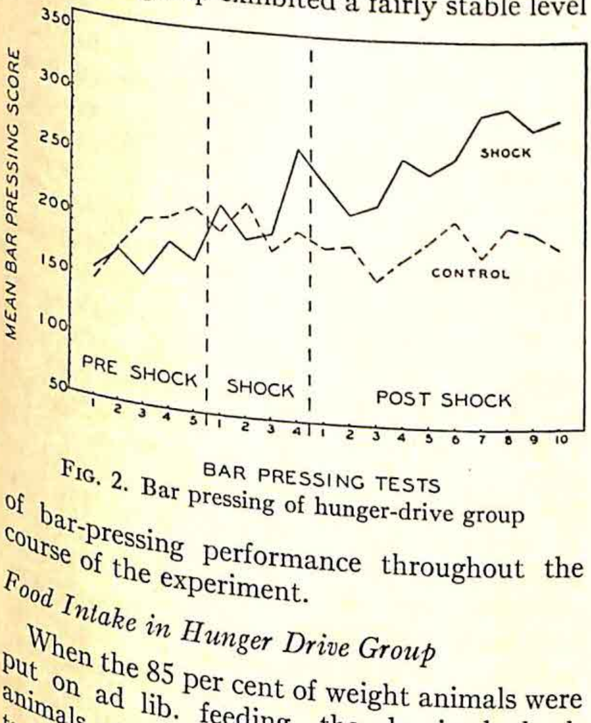

FIG. 2. Bar pressing of hunger-drive group

Food Intake in Hunger Drive Group

When the 85 per cent of weight animals were put on ad lib. feeding, the deprived shock animals ate significantly more than the controls ($t = 2.195$, $p < .05$ for one tail). These data show that the difference in results between the deprived and ad lib.-fed experimental animals is not an artifact of the different measures used. Both measures applied to the 85 per cent of weight group indicate that hunger drive is *increased* in the deprived shocked animals. This is opposite to the findings in shocked rats on an ad libitum schedule.

Activity

Hunger drive group. The question arises as to whether the increase in bar pressing of the shocked animals merely reflects a rise in their activity level rather than increased hunger drive. The activity measures summarized in Table 3 indicate that this is not the case. The differences between the activity measures of the 85 per cent of weight shock and control groups do not approach significance either before or after shock. Furthermore, the activity of the 85 per cent of weight shock group is not significantly different from that of the controls in the postshock period, as compared with the preshock period, while its bar-pressing scores are greatly increased as compared with the preshock period. It would not be expected that shock would act to increase activity since Stone (10) and Winder (11) report that the effect of shock is to decrease spontaneous locomotor activity. It would therefore seem that the increased bar pressing of the shock group is not explainable in terms of a concomitant increase in activity level.

TABLE 3

Average Pre- and Postshock Activity Measures, Hunger Drive and Food Intake Groups

(The measures below are in terms of mean drum revolutions per day)

GROUP	N	10 DAYS PRE-SHOCK	t	p	23 DAYS POST-SHOCK	t	p
Hung. drive shock	5	4592.6	1.12	<.30	5368.3	.526	>.60
Hung. drive control	6	2873.7			4473.5		
Food intake shock	5	604.8	.448	<.60	305.2	1.03	>.30
Food intake control	6	500.5			468.8		
Food intake shock pre-post *Difference*	5	309.6	1.87	<.10			
Food intake control pre-post *Difference*	6	31.6					

Food-intake group. Before shock there is no significant difference between the shocked and the control ad lib. animals. Following shock, the shocked animals are less active. The difference between the preshock-postshock differences approached significance and confirms the finding of Stone (10) and Winder (11). The activity measures of the ad lib. group are more comparable to the findings of previous workers since previous studies used ad lib. feeding.

The results indicate that there is no simple relationship between activity and eating in the shocked rat. Whereas the activity of the ad lib. shocked animals decreased when their food intake decreased, it remained lower for the duration of the experiment, after the differences between the food-intake scores of the shocked and control animals had disappeared. Furthermore, the changes in hunger shown by the 85 per cent of weight shocked animals did not parallel the changes in activity (as compared with the controls). It may be that hunger and activity in the shocked rat vary together when at first both fall below the normal level but that this relationship is not maintained in time and does not obtain for levels of hunger drive above normal.

DISCUSSION

The results of this study indicate that the experimental manipulation of feeding, instituted to permit the study of hunger drive and food intake separately, resulted in two different effects of shock. When animals were maintained on a diet that kept them underweight by a constant amount, shock acted to *increase* motivation for food as measured by bar pressing and subsequent ad lib.-feeding tests. If the animals were allowed to feed ad libitum, however, the effect of shock was to *decrease* motivation for food, as measured by food intake, for some time after shock and to produce a long-lasting, albeit insignificant, decrement in body weight.

These results have relevance for the studies of the effect of shock on maze behavior where food reward is used as the motivation to perform. Since it is generally agreed that habit strength is a function of hunger drive, a rat's maze performance will depend in part on hunger drive. If shock produces only the two effects described above, shocked animals that are underweight would be hungrier than controls, and would therefore perform better. Similarly, shocked animals that are allowed sufficient time to eat to permit them to maintain weight and exhibit some daily gain would be less hungry than controls and therefore perform less well. However, the water-maze behavior of the convulsed rat (2, 3) indicates that shock also acts to produce a deficit in performance that is independent of hunger. This would suggest that in addition to its effect on hunger drive, shock also affects motivation to escape from water. However, it is probably simpler to assume that shock somehow acts to impair learning or retention generally. Thus, in the shocked animals whose diet has been restricted, the increased hunger and impairment in learning would tend to cancel each other, and their performance might not differ from that of the controls. In ad lib.-fed animals, however, both drive and learning capacity would be reduced following shock. The combined effect of the two would be to worsen performance.

It would be expected, then, that in studies in which shocked animals were deprived of food, a deficit in maze performance may not have been observed. Conversely, in studies in which the shocked animals were allowed to feed ad libitum or sufficiently to maintain weight, an impaired performance may have been observed. The literature on the effects of ECS has been examined in the light of this formulation.

The following two studies appear to confirm directly the above hypothesis. Bernberg (1), working with the Stone multiple-T maze, reports that rats given convulsive shock are significantly inferior to controls in number of errors. Using a closely similar maze, the 14-unit elevated multiple-T, McGinnies (7) reported no significant increase in errors at any time on the part of his shocked animals. There are a number of differences between the two studies. However, McGinnies, who got no deficit, kept his animals at 85 per cent of weight throughout the experiment. Bernberg, who found a deficit, allowed his animals to feed for 1 hr. (sufficient to maintain weight) following daily training and in fact reports that his shocked animals ate less than the controls following shock.

The following two studies offer less direct confirmation, but the general trend of the results is consistent with the present findings. Horowitz and Stone (4) report that the effect of shock was to disrupt a light-discrimination habit during the shock period but not in the immediate postshock period (10 days). Furthermore, in the learning of a new habit after this 10-day period, no difference could be discerned between the two groups. Horowitz and Stone concluded that full recovery from the effects of shock (as measured by this habit) will take place within 10 to 50 days after shock. This result is not in agreement with the later findings of Braun, Russell, and Patton (2, 3), who found significant impairment in learning and retention immediately after shock and 90 days postshock. Braun *et al*. used a water maze (Lashley III) so that their results are independent of changes in food motivation. However, Horowitz and Stone used food reward, and their feeding is described as "a daily ration . . . to permit a slight gain on the part of each animal during the course of the experiment" (4, p. 15). In young growing animals this, in effect, was restricting their weight. Thus, it may be that the shocked rats were hungrier than the controls in the postshock period since the present study indicates a long-lasting increase in the hunger of food-deprived animals postshock. The added motivation may have had the effect of obscuring their deficit in performance. This is not a consideration in the Braun, Russell, and Patton study because they used a water maze.

It has been shown how the phenomenon reported in this paper relates to previous research on ECS and may be used to reconcile differences between the findings of various investigators. The implications of this are twofold. First, in terms of methodology it will be necessary, in any ECS study where food-motivated responses are involved, to specify exactly the conditions of feeding, for this affects motivation. Second, in order to compare validly the performance of shocked and control animals in any situation, it must be demonstrated that the drive states underlying the behavior that is measured are really comparable in the two groups. Moreover, in any research that involves relating behavior to physiological intervention such as cortical extirpation, drug injection, convulsive shock, oxygen deprivation and the like, the treatment should be demonstrated not to affect motivation to perform before changes in performance are attributed to impairment of some other function.

SUMMARY

In an investigation designed to study the effect of shock on eating behavior in the white rat, it was found that animals that were kept at 85 per cent of weight during and after shock showed a significant increase in hunger in the postshock period as measured by bar pressing and subsequent ad lib.-feeding tests, whereas shocked animals that were allowed to feed ad libitum showed a long-lasting decrement in body weight and activity and ate significantly less during the first ten-day period postshock. The relevance of this finding for previous studies of shock was indicated, and the necessity for studying the effects of physiological intervention on motivation was stressed.

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EDITORIAL NOTE

The article entitled "Effects of Cortical Lesions on Maze Retention by the Rat" by Burton S. Rosner in the February 1953 *Journal of Comparative and Physiological Psychology*, pages 56–60, contained a footnote (Footnote 3) stating that Table 3, an analysis of thalamic degeneration and subcortical damage, had been deposited with the American Documentation Institute, but that it had been lost by the ADI. We are happy to report that the ADI has now found the missing table. To obtain the table, order Document 3929 from the ADI Auxiliary Publications Project, Photoduplication Service, ℅ Library of Congress, Washington 25, D. C., remitting $1.25 for microfilm (images 1 in. high on standard 35-mm. motion picture film) or $1.25 for photocopies readable without optical aid.

MAZE PERFORMANCE OF RATS UNDER CONDITIONS OF SURFACE AND UNDERWATER SWIMMING[1]

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An underwater swimming maze provides a situation in which motivation to escape is augmented by an inexorable need of oxygen. Thus the urgency to reach an exit where normal breathing can be resumed is superimposed upon the usual escape-from-water incentive. In this study the problem to be investigated has a double aspect: (*a*) Does heightened "drive" of the kind afforded by an underwater maze facilitate or retard rate of mastery? (*b*) To what extent are maze habits that were formed either by underwater or by surface swimming disrupted when the animals are required to reverse the mode of swimming?

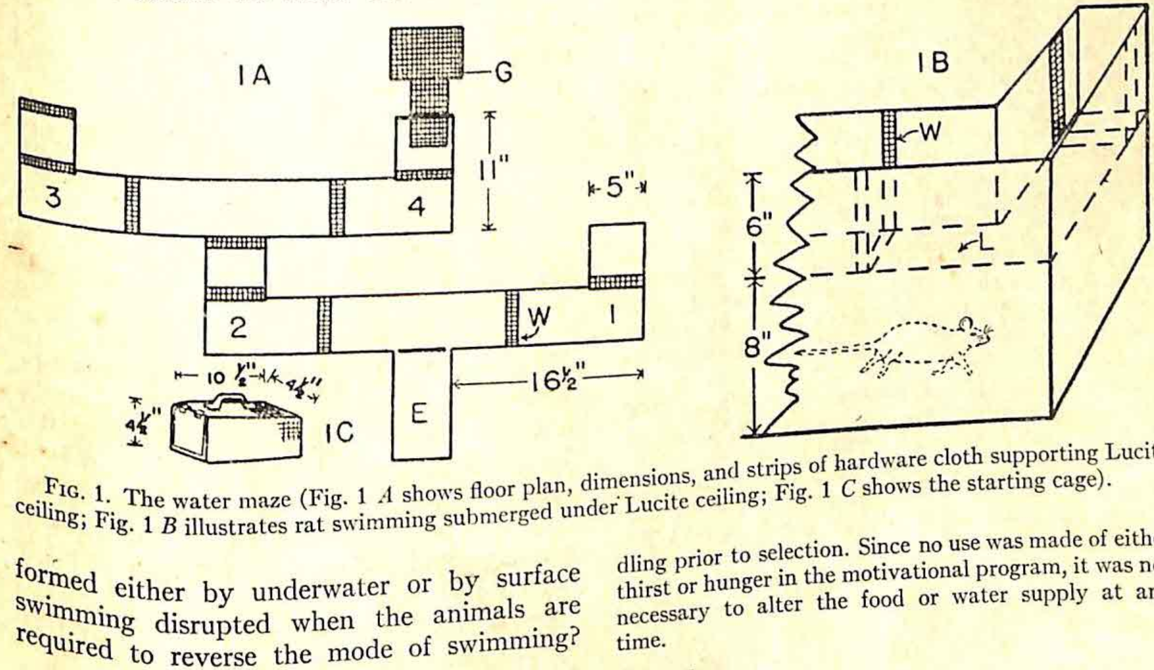

FIG. 1. The water maze (Fig. 1 *A* shows floor plan, dimensions, and strips of hardware cloth supporting Lucite ceiling; Fig. 1 *B* illustrates rat swimming submerged under Lucite ceiling; Fig. 1 *C* shows the starting cage).

METHOD

Apparatus

Two sheet-iron mazes of the Warden-U type, set in a tank of water 8 in. deep, were used (see Fig. 1*A* and 1*B*). The dimensions and floor plans of these mazes are identical. To enforce underwater swimming in one of them, Lucite strips of appropriate width and length were suspended approximately 7 in. above the floor in all parts of the maze except the starting well and a portion of the terminal unit near the escape ramp. Use of two mazes, one for underwater swimming and one for surface swimming, obviated the necessity of removing and replacing the artificial ceilings to accommodate animals of different groups. The starting cage (Fig. 1*C*) is made of hardware cloth and fits snugly into the starting well. Retracing into this cage is prevented by a vertical sliding door, belonging to the maze, which is closed as the animal leaves the cage.

Animals

Twenty-one adult albino rats were used; of these 12 were females and 9 were males. None had been on a learning task before, but all were accustomed to handling prior to selection. Since no use was made of either thirst or hunger in the motivational program, it was not necessary to alter the food or water supply at any time.

Procedure

Preliminary swimming. Twenty adaptation trials were given each rat in a 10-ft. straightaway alley, at the rate of five per day. The first ten trials allowed swimming on the surface of the water and were introduced to acquaint the rats with escape by swimming to a goal, to reduce futile attempts to climb out, and to familiarize them with the exit ramp. The next ten trials entailed underwater swimming from the starting cage to the ramp; in these trials the rats became acquainted with "holding the breath" under water. Those that loitered may have experienced some degree of "panic" as the threat of acute anoxia was experienced. The rats were handled in groups of five, each taking its turn until five trials had been completed.

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Early preliminary trials were characterized ofttimes by attempts to climb the metal walls, to grasp the upper edge, or by frantic efforts to leap out of the water. Occasionally, an animal would dive and swim submerged for a few feet. After a few trials, however, the animals usually swam directly to the ramp without waste effort excepting, possibly, a brief delay and circling just after leaving the starting cage. As soon as an animal reached the goal ramp, it was "stripped" gently of excess water and replaced with its group to await the next turn. Introduction of a ceiling, made of ½-in. mesh hardware cloth, on the eleventh trial to enforce underwater locomotion led to a considerable amount of frantic paddling, retracing, and vigorous attempts to push through this covering. These tendencies gradually abated, however, with the result that by the twentieth trial most animals moved from starting cage to goal ramp with little delay.

Original and transfer maze trials. Animals were distributed into two groups: Group A ($N = 11$), which began by underwater swimming, and Group B ($N = 10$), which began by surface swimming. Trials were continued on the original assignment at the rate of 5 per day until all had a minimum of 25 trials. Since that number was sufficient for mastery of the maze by many of the surface swimmers, this phase of training was terminated for those which had made four perfect swims in a block of 5 consecutive trials. Those requiring more trials to meet the criterion were continued until this was reached. Either after trial 25 or after the criterion of mastery of the original problem had been achieved, the transfer problem was introduced. With this change, underwater learners were permitted to swim the maze on the surface, and surface swimmers were transferred to the underwater condition. Following transfer, each rat received 5 trials daily for a minimum of 10 trials. If within that series the criterion of 4 perfect out of 5 trials had been met, tests were terminated; if not, training was continued until the specified criterion had been achieved. Thus, all rats of Groups A and B had, as a minimum, 10 transfer trials.

Again, animals were handled in groups of five, on a rotational basis that allowed from about 10 to 12 min. between individual trials. By supplemental heat the temperature of the maze room was raised to approximately 85°F. each day before the trials began. The temperature of the water, however, remained within the range of from 61° to 66°F.

To begin a trial, the starting cage, with animal inside and front door open, was allowed to settle down in the starting well until it rested on the bottom of the maze. A vertical sliding door at the end of the starting well prevented the animal's starting until the cage had dropped below the water line; thus, each animal of both groups had to start from a submerged position. The elapsed time from departure to arrival at the foot of the ramp was recorded for each trial.

Errors. Errors were of two general types: (*a*) Forward-going, or entrances into wrong culs, and (*b*) retracing beyond what was necessary to escape from a blind cul-de-sac. As may be noted from Fig. 1*A*, entries into alleys 1 and 3 constitute forward-going errors. Retracings consist chiefly of swims from 2 to 1, 3 to 1, 4 to 3, or 4 to 1. No error was tallied if an animal, while partly in the starting cage, moved its head and shoulders in the direction of alley 1 or alley 3, or even if it turned around just outside the exit.

RESULTS

Original Learning

The first comparisons are based on original learning of Group A (underwater), whose data are designated in the table and graphs by the symbols *A-o-u*, and Group B (surface) for which the analogous symbols are *B-o-s*.

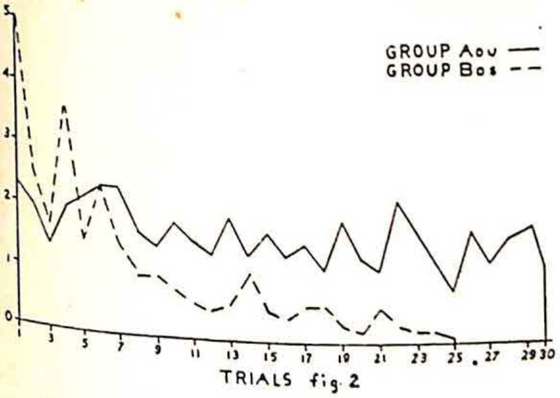
TABLE 1

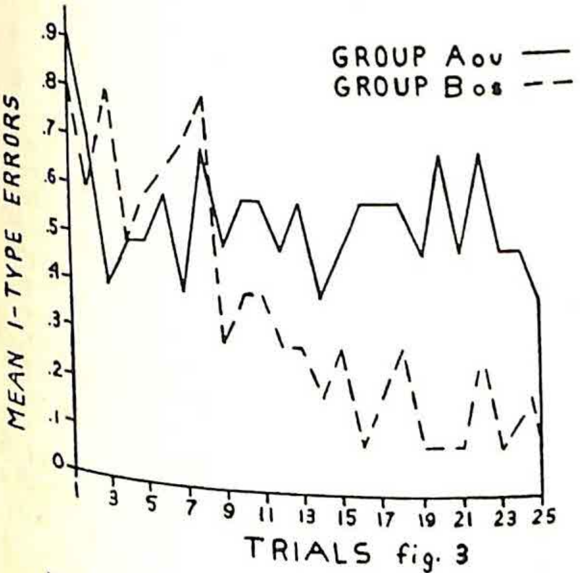
Maze Learning and Transfer Performance of Underwater- and Surface-Swimming Rats (N of Group A = 11; Group B = 10)

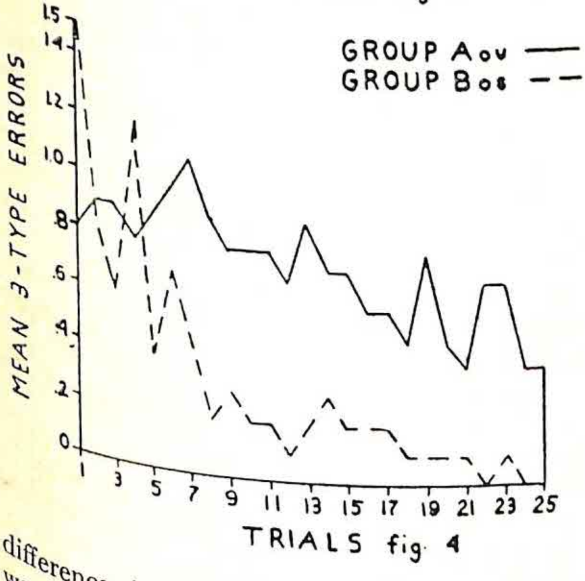
		A-o-u	*B-o-s*	*p*
Means, Original	Trs. to Master	39.45	11.20	.001
	E on trs. 1–25	43.45	28.00	.05
	E on trs. 1–5	9.64	14.40	.05
	E on trs. 6–25	33.45	14.70	.001
		A-t-s	*B-t-u*	*p*
Means, Transfer	Trs. to Master	5.45	25.90	.01
	E on trs. 1–10	5.45	16.30	.001

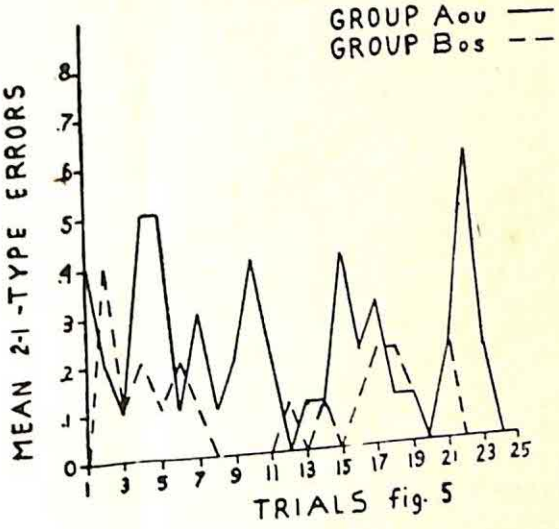
Mastery. As shown in Table 1, the mean number of trials for mastery is significantly larger for A-o-u than for B-o-s ($p < .001$). Most of the latter had not met the criterion of mastery within their obligatory block of 25 trials, whereas 80 per cent of the surface swimmers had satisfied the criterion within that number of trials.

Errors. Both qualitative and quantitative differences in errors appear in records of the underwater and surface swimmers. For the first 25 trials the difference in means favors group B-o-s ($p = .05$). As shown in Figure 2, however, the mean for Group B was higher than that of Group A at the outset (trials 1 to 5), a difference that is significant at the .05 level. As shown in Figures 4 and 6, it is due chiefly to an excess of entries into cul 3 and retracings from 3 to 1. For trials 6 to 25 the direction of the difference is reversed and significantly favors Group B-o-s ($p < .001$). Small, irregular differences appeared in the 2 to 1 type of retracing, as shown in Figure 5, but these differences are not significant. Because of the quantitative and qualitative differences in errors one may infer that underwater swimming prompts a somewhat different approach to solution of the escape problem from that prompted by surface swimming.









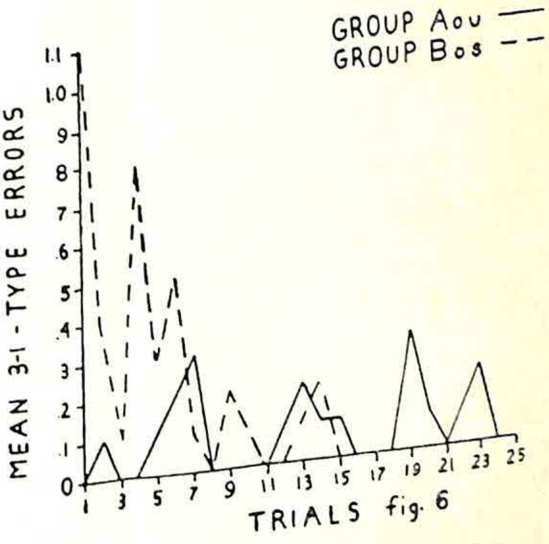


FIG. 2 to 6. Error curves for original learning

Transfer Performance

All rats made the transfer on trial 26 if they had met the criterion of mastery prior to that time, but if not, they made the shift on the next trial following this achievement. Their transfer records are designated by the symbols *A-t-s* and *B-t-u*, respectively.

Mastery after transfer. The appropriate data of Table 1 show that mastery after transfer was achieved in significantly fewer trials by Group A-t-s than Group B-t-u ($p < .01$). Clearly, the change from underwater to surface conditions interfered less with correct choices of pathways than the change from surface to underwater swimming.

Errors. As shown in Figure 7, a clear-cut difference between group means appeared on the first trial, and the divergence increased immediately thereafter. Especially interesting is an increasing number of type-1 errors made by Group B-t-u during the first ten trials, as shown in Figure 8, and prolonged difficulty the animals had with this wrong turn. This curve resembles somewhat that of Group A-o-u in its original learning when swimming underwater (see Fig. 3). For Group B-t-u the type-3 error also was frequent, but this alley was mastered more rapidly than was alley 1 (compare Fig. 8 and 9).

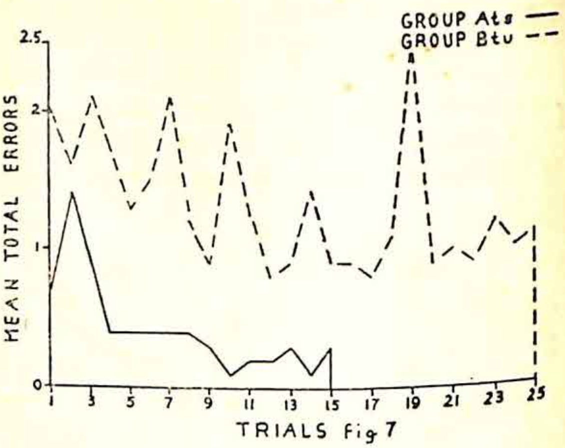
The difference between total number of errors made by Groups A-t-s and B-t-u on trials 1 to 10, in which all animals were present, is significant at the .001 level. Differences in type-1 errors are not significant for trials 1 to 10, but those for type 3 are significant at the .001 level.

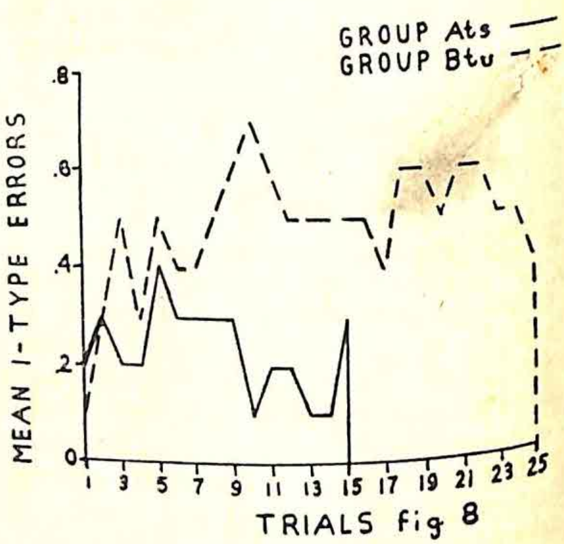
Underwater Original Compared with Transfer Records

Here the primary interest is that of estimating savings by Group B-t-u in swimming the maze correctly underwater by virtue of previous mastery by surface swimming. To do this, their transfer record is compared with the original learning of A-o-u. They required on the average 25.9 trials to satisfy the criterion of mastery; this was 13.5 trials less than required by Group A-o-u, which first mastered the maze by underwater swimming. This apparently large difference is not significant ($p =$ .1). In Figure 10, the means for errors by Groups A-o-u and B-t-u for the first 15 trials of underwater swimming are represented. The graphs are terminated at trial 15 because some animals of Group B began to drop out at this time by virtue of meeting the criterion of mastery. It is obvious that transfer from surface to underwater swimming greatly disturbed the habits of Group B.

Surface Original and Transfer Compared

Group A-t-s, when transferred from underwater to surface swimming, achieved the criterion of mastery in 5.45 trials. Group B-o-s had required 11.20 trials to meet this criterion in its original learning period. Figure 11





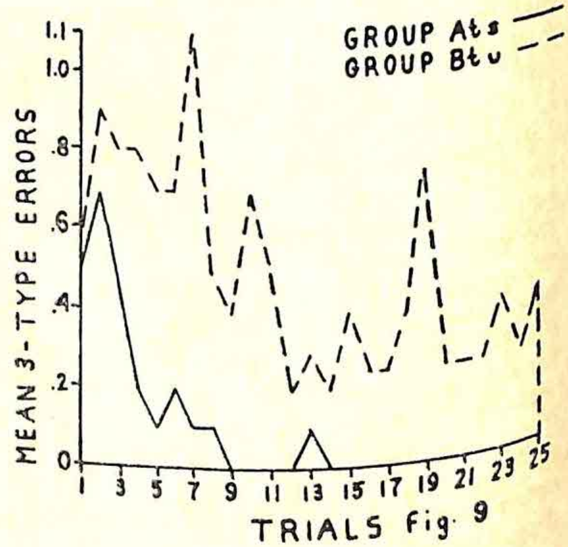


FIG. 7 to 9. Error curves for transfer trials graphically illustrates the mean number of errors made by the two groups while all were participating in the trials. From this and Figure 10 it is evident that less disruption, by far, arises when animals are transferred from underwater to surface swimming than when the order of transfer is the reverse.

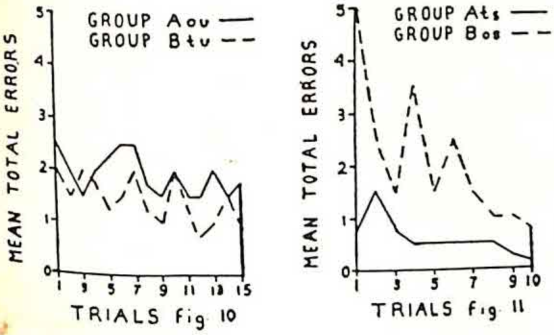


FIG. 10 and 11. Comparative error curves for original and transfer trials

DISCUSSION

The foregoing evidence clearly demonstrates that learning a two-unit Warden-U maze by surface swimming proceeds more rapidly than learning the same maze pattern by underwater swimming. Also, the performance of rats that have mastered the maze by surface swimming is disorganized much worse than that of rats which are shifted from underwater to surface locomotion. Assuming that a fundamental difference in potential learning ability of the groups is not in question, what hypotheses may be offered to account for these differences?

Optical cues. The experimental room was well lighted by windows halfway from ceiling to floor across one end of the room, and by two 150-w. lamps, suspended directly above the mazes at a distance of about 6 ft. from the water. Whenever agitation of sediment made the water somewhat murky, old water was drawn off and fresh water added; also, if scum condensed on the Lucite ceiling, it was removed. These precautions gave reasonable assurance that underwater swimmers, readily seen by the *E* through the Lucite cover, could make some use of lights and shadows for general orientation while swimming. To what extent near and distant objects could be seen distinctly is not known, however.

Units of the two mazes were similarly constructed of sheet metal which bore no distinctive markings. Hangers for the Lucite ceilings were symmetrically placed in each unit of the maze, hence these offered neither misguiding nor helpful cues to the underwater swimmers. All things considered, we incline to the belief that a difference in opportunity to use visual cues does not account for the obtained differences in original learning by Groups A and B, nor in the performance following transfer. Nonetheless, in order to determine what positive or negative value vision may actually have in this situation, supplementary studies are needed in which both surface and underwater swimmers are required to simulate the training program of our present groups after obscuration of visual cues by darkening the pathways or after blinding the rats.

The fact that normal rats in darkness, and also totally blind rats, have been able to learn certain complex dry-floor, alley mazes with little or no evidence of handicap is relevant to the discussion, but the weight of evidence is diminished by our knowledge that similar groups of rats usually suffer considerable handicap both in learning and in transfer on narrow-tread, elevated mazes.

Anoxia. Certain studies (1, 4, 5, 6, 7) have shown that animals when required to learn or perform in an oxygen-deficient environment are somewhat disturbed or retarded; hence, the hypothesis that acute lack of oxygen may have been responsible for inferior learning and transfer in underwater swimmers deserves consideration.

To the authors' knowledge, no studies in which oxygen deprivation has been employed as a "drive condition" in rats have been reported in the literature on maze learning. Experiments such as those of Hurder (2) and Shock and Scow (6) deal with relatively prolonged or chronic exposure to conditions in which the inspired air contained less than the normal amount of oxygen and thus are not strictly comparable to the present experiment in which the *S* is merely required to "hold its breath" while swimming. Probably only mild oxygen deficiency occurred as a general rule, since most animals, at worst, traversed the maze in less than 60 sec. Moreover, it seems unlikely that such anoxia as did occur would so damage brain function as to induce confusional states or to impair learning and retention on a physiological basis. The condition is essentially like that of a human runner, swimmer, or weight lifter who holds his breath during brief periods of maximal effort but suffers no intellectual impairment therefrom.

No proper check on the cogency of the anoxia hypothesis has been made in this laboratory. Relevant to the question, however, are data from five rats in Group A which began to show signs of distress after swimming underwater for between 1 and 1½ min. and had to be removed from the maze to prevent drowning. The mean of their maze records is only slightly inferior to that of others that managed to effect escape without any evidence of distress. Further studies should be made in which there is submersion for various periods of time just before maze trials for both surface and underwater swimmers. These would provide evidence on the effects of brief breath-holding on maze learning.

"Panic." A hypothesis that appeals to human experience and also accords with observations of the underwater swimmers pertains to emotional disturbance in the category of mild "panic" that sometimes appeared when the animals were forced to submerge. This may have interfered with the requisite deliberative control that is needed for learning a maze or for the execution of correct maze habits previously acquired. In preliminary trials some rats showed signs of this type of emotional disturbance by hyperactivity and defecation. A few animals manifested special symptoms, such as squealing when touched, or diving back into the water after climbing the ramp at the end of the straightaway. Moreover, early underwater trials in the maze were characterized by vigorous attempts to push up through the cover. This was true of the transfer animals as well as those just beginning. There was also some excess movement of legs which might indicate mild "panic" or confusion. Unlike the usual exploratory entries into blind alleys or retracing over portions of the true path, errors were frequently committed in a slapdash fashion, and were repeated so often in certain instances that drowning was actually a danger.

Repetitive errors on the part of certain animals in the underwater maze gave the impression that there might be in this situation a form of "stereotypy" analogous to that described by Maier (3) when working with rats faced with a frustrating problem, e.g., an insoluble or difficult discrimination. Maier concluded that normal learning and frustration-linked learning are qualitatively different and require different explanatory principles. The frustration-induced response is described as rigid, unadaptive, and stronger than a response normally learned, despite the fact that the learned response is rewarded and the frustrated response is not.

This view of the disorganization of learned responses in the case of animals transferred from surface to underwater conditions has merit, at the descriptive level, if instead of the Maier type of frustration one thinks of "panic"-instigated behavior. Noteworthy is the relatively poor performance of Group B when required to traverse the maze under water. Wrong turns again became prevalent, and some animals that appeared to be near mastery in the transfer situation adopted wrong turns and continued them for long periods of time, despite their maladaptiveness.

The authors believe that many techniques requiring underwater swimming, as in discrimination, delayed reaction, detours, "reasoning," manipulative problems, etc., will be very instructive in defining the role of "panic"-instigated behavior both in learning and in the execution of learned responses.

SUMMARY AND CONCLUSIONS

1. In original learning of a two-alley swimming maze, a group of rats required to swim under water required more trials for mastery and made significantly more errors than a comparable group of surface swimmers.

2. When surface learners were required to demonstrate mastery again by underwater swimming, and underwater learners by surface swimming, the net savings in terms of trials and errors were positive in both instances, but the change from underwater to surface was far less disruptive than a shift in the other direction.

3. Original learning by underwater as opposed to surface swimming produced qualitative differences in the types and frequencies of errors most persistently made. Likewise,

transfer after maze mastery from one to the other type of swimming produced qualitative differences in the error patterns.

4. Of three hypotheses tentatively introduced to account for the observed differences—availability and use of visual cues, anoxia, and mild "panic" aroused by enforced suspension of breathing—the authors regard the latter as most promising to account for behavioral differences that gave rise to the relative inferiority of underwater swimmers.

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INTEROCULAR TRANSFER OF HABITS LEARNED MONOCULARLY IN VISUALLY NAIVE AND VISUALLY EXPERIENCED CATS

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Evidence for the contribution to visual perception of the early visual environment has emphasized the importance of patterned stimulation (3, 11). The present study undertook to determine whether early learning is a factor in the behavioral equivalence of the two eyes in discriminations made with either eye alone. The question asked in this experiment was: Will a discrimination habit learned through vision with only one eye be retained when tested for with only the other eye open, if the second eye has not previously been exposed to visual patterns?

The phenomena of rivalry, dominance, and fusion imply that in man the two eyes may operate independently, in competition, or cooperatively. The neurological correlates of these differing modes of interaction are not known, beyond the fact that corresponding retinal areas must be stimulated to permit fusion. Binocular projection paths of "corresponding points" to the same region of the occipital cortex presumably furnish the basic neuroanatomical convergence of pathways for fusion and equivalence of stimulation.

The very occurrence of rivalry demands some central independence of stimulation from the two eyes. Yet the world looks the same (to most of us) when seen with either eye. This perceptual equivalence may not be fully provided for by innately given neurophysiological relations. In the experiment reported here this possibility is tested by preventing binocular pattern vision until after behavior has come under the control of vision through one eye, then testing for such control with the other eye. Since the use of continuous darkness produces retinal anomalies in some vertebrate eyes (11, 16), a method used with infant chimpanzees (11, 12) to allow diffuse light of all wave lengths to enter the eyes for regular periods, daily, was adapted to the needs of the present study.

METHOD

Subjects

Twelve kittens, 6 in the experimental group and 6 in control groups, provided the data of this study. The experimental group came from three litters, designated as litters A (born 2/19/50), B (born 2/22/50), and C (born 5/20/50). The litters consisted at birth of 3, 3, and 5 kittens, respectively. One kitten from litter A died the day after birth. Two kittens of the C litter were used in other experiments, and the remaining 8 kittens were originally intended to constitute the experimental group. However, a laboratory epidemic of enteritis and respiratory infection in October, 1950, took the lives of 1 kitten from A litter (A-1) and 2 from C litter (C-3 and C-4). One of these (C-4) had by this time completed training on the original monocular habit (Table 1). Another, A-1, had received 1260 trials on the form discrimination habit without meeting the learning criterion. C-3 died after a brief illness, prior to which it had worked for 200 trials on the brightness discrimination habit without approaching the criterion. Except for the period of illness, which lasted approximately ten days in the cats that recovered, the animals were in good health.

The control groups were from two litters of 4 kittens each; the D litter was born on 7/15/50 and the 2 home-reared kittens, Ivan and Tia, were born on 10/23/50.

Apparatus

The discrimination-learning apparatus was our version of a commonly used modification of the Yerkes-Watson box, in which the animal walks directly into one or the other of the cues to be discriminated. The box was narrow (15 cm.) at its entrance, 76 cm. long, and 46 cm. wide at the end containing the stimulus doors. A partition extended forward 15 cm. between the doors. The stimulus doors were hinged from the top and consisted of clear Plexiglas 16.5 cm. square. Slots along the side and lower margins of the back surface of the stimulus doors permitted the rapid placement and removal of stimulus cards. A locking device made possible the barring of either door so that only one door (that carrying the positive stimulus) could be pushed open by the animal. Food was placed so that the cat could eat after pushing head and shoulders through the flap door.

Four pairs of stimulus cards were used. The first pair presented a circle on one card, an equilateral triangle with lower margin horizontal on the other. These figures were solid black painted on a light gray background, the area of each figure being 24 sq. cm. The second pair employed the same sizes and shapes of figures, but was made so that transmitted light coming through white tissue paper produced a high-contrast white figure on a dark surround. The white figure had a luminance of 2.6 ft.-L. During use of this pair of cards illumination of the front area of the apparatus was kept at a low (human) photopic level, just high enough to permit observation of the animal.

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A third pair of cards was painted with alternating black and white stripes, horizontal on one card and vertical on the other, each stripe 1 in. wide. The fourth pair of cards was for training and testing a brightness discrimination habit. On each card a cut-out X, 31 sq. cm. in area, with each cross arm measuring 2.5 cm. by 7.5 cm., was covered with white tissue paper. The luminance of the brighter was 2.5 ft.-L., and the other was approximately 0.9 ft.-L.

Procedure

The three litters of kittens from which the experimental animals came were moved into a darkroom with their mothers a few days after birth and before the eyes had opened. Weaning was begun at 8 weeks, and at 14 weeks of age the kittens were brought out for 30 min. daily, wearing a hood, for the purpose of giving light exposure to both eyes, but pattern vision to only one. The hood had an opening for mouth and nostrils, a white translucent Plexiglas insert over the eyes, and was tied in place with a drawstring running under the jaw and behind the ears. The Plexiglas insert was curved around the contour of the face, had a circular opening for clear vision for one eye, and a low ridge fitting snugly along the nose between the eyes. It was approximately 3 cm. high and 6 cm. wide. During the daily period in the light, the kittens played with each other and were fed a daily ration of meat, which was later used as reward in the learning task. Feeding was done from a small dish placed in one end of an enclosed area of the same dimensions as that through which the animals later approached the stimulus cards in the training apparatus. The position of the dish was randomly varied between the two places which would be directly in front of the stimulus cards in the training apparatus. Separate small portions of meat were put into the dish, until the cats "found" the dish about 20 times on a given day.

When the animals were 17 weeks (litter C) or 20 weeks (litters A and B) of age, training was begun on a visual discrimination habit. Average daily time in the light was increased to 60 min. (range: 30 to 90 min.). These discrimination habits were different for each of the experimental animals and sampled three classes of distinguishing cues: geometrical form, direction of striped lines, and brightness. One cat, B-2, was given 1320 trials with the triangle (+) and circle (−) as cues. She failed in this time to respond to the triangle beyond a chance level, developed a strong position preference, and then sat motionless in the apparatus for progressively longer periods. After a rest interval of 6 weeks, during which she continued to play in the light with hood on for 60 min. daily, she was started on the horizontal- vs. vertical-lines problem.

The criteria of learning for the initial habit were either (*a*) two successive sessions of 20 trials each at a level of 90 per cent correct or better on each session, or (*b*) 10 successive sessions of 20 trials at a level of 85 per cent correct or better on each session. Training was given 10 trials daily for the first 100 trials and then 20 trials daily. The correction method was used for the first 600 trials. When a habit was not learned in this number of trials, the noncorrection method was substituted, except in the case of animal A-2. With the three B-litter *S*s, strong position habits were effectively counteracted after 1160 trials by a "guiding" procedure used for several sessions. This consisted in placing a small transparent Plexiglas barrier just beyond the choice point on the error side of the apparatus. It was repeated after 1440 trials with B-3.

Up to the time of "mastery" of the first habit to the level of the arbitrary criterion, training was given in one morning session daily. On the morning after mastery, the position of the Plexiglas insert in the hood was reversed to expose the other eye. (The original training eye was now covered with translucent Plexiglas.) A session of 20 trials was given. That afternoon, 5 hr. later, a session was given with the original eye exposed. This became the daily schedule until performance in the newly exposed eye reached a level of 85 per cent correct or better on each of two successive 20-trial sessions.

The control *S*s, Ivan and Tia, also began training at 20 weeks of age. These two *S*s had lived as house pets with unrestricted vision until shortly before the training schedule was started, when they were moved into the laboratory. About five days were required to accustom these animals to feeding while wearing the hoods. They were then trained on the triangle vs. circle habits, monocularly. After showing complete transfer to the other eye on this habit, they were trained on the horizontal- vs. vertical-lines problem, the eye used for training being reversed (see Table 1).

Four control animals (the D cats) were raised in a lighted laboratory cage of the same size as used for the experimental group. Training was begun at 15 weeks of age. These animals learned habits binocularly, not wearing hoods. Two of these learned brightness habits first, and two the circle vs. triangle habits. Then each cat learned a second habit with the other pair of discriminandae.

RESULTS

The basic question asked in this experiment is answered from the data of five *S*s listed in Table 1. All animals whose total previous visual-pattern stimulation in one eye had been extremely restricted by the use of a Plexiglas diffusing "goggle," showed inability to respond in a discrimination problem when use of this eye had to be substituted for that of the eye used during training. The average performance

TABLE 1

Numbers of Trials Required to Meet the Criteria of Learning on Each Discrimination Problem

CAT	STIMULI TO BE DISCRIMINATED	TRAINING EYE	CRITERIA	TRIALS TO MEET CRITERION	TRIALS TO CRITERION IN 2ND EYE[1]
	Experimental Group				
A-2	black *triangle* (+) vs. black *circle*	L	200 trials	1840	280
B-1	white *circle* (+) vs. white *triangle*	R	40 trials	1490	160
B-2	*horizontal* (+) vs. *vertical* stripes	R	200 trials	1920[2]	120
B-3	black *circle* (+) vs. black *triangle*	R	40 trials	1660	520
C-4	*light* grey (+) vs. *dark* grey "X"	R	40 trials	380	
C-5	*dark* grey (+) vs. *light* grey "X"	L	200 trials	600	180
	Control Groups (First problem)				
Ivan	white *triangle* (+) vs. white *circle*	R	40 trials	360	40
Tia	White *circle* (+) vs. white *triangle*	L	40 trials	180	40
D-1	black *circle* (+) vs. black *triangle*	both	40 trials	220	
D-2	*dark* grey (+) vs. *light* grey "X"	both	40 trials	180	
D-3	*light* grey (+) vs. *dark* grey "X"	both	40 trials	260	
D-4	white *triangle* (+) vs. white *circle*	both	40 trials	180	
	Control Groups (Second problem)				
Ivan	*vertical* (+) vs. *horizontal* stripes	L	40 trials	80	40
Tia	*horizontal* (+) vs. *vertical* stripes	R	40 trials	100	40
D-1	light vs. dark "X"	both	40 trials	200	
D-2	white *triangle* (+) vs. white *circle*	both	40 trials	60	
D-3	black *circle* (+) vs. black *triangle*	both	40 trials	440	
D-4	dark vs. light "X"	both	40 trials	120	

[1] Criterion for learning in 2nd eye: 85% correct or better on each of the two consecutive 20-trial sessions. Figures in the last two columns include the 40 (or 200) trials during which the criteria were met.

[2] This figure includes 1320 trials on triangle vs. circle.

for all five cats on the first 60 trials with the second eye was 56 per cent correct, or not significantly different from chance. However, there was a very large saving in the number of trials necessary for "relearning." The generality of this finding is indicated by the similarity in the data for all three visual-stimulus dimensions. Even the brightness discrimination habit was not transferred (animal C-5). Results with the control animals, Ivan and Tia, show that in the normally reared cat a habit learned with one eye open can be mediated through the other without any drop in performance. In fact, with control *S* Tia, the first errorless session was the first transfer session.

All the experimental animals showed some general disturbance of behavior when use of the second eye was begun. They bumped into the partition or walls of the box, moved slowly, sometimes with long pauses, twitching of the tail increased, and the final choice was made with marked hesitation. All this made the session of 20 trials take longer than had been the case during the previous days. Much of this behavior carried over into the afternoon session with the previously trained eye. The degree of carry-over varied somewhat from animal to animal.

The initial habit (performance with the original training eye) broke down in three of the five cats following the first session with the unpracticed eye. Both animals (A-2 and B-2) that maintained performance with the practiced eye were on the "overtraining" schedule; that is, they had performed for 200 trials or more with a high level of accuracy on the practiced eye before being confronted with the transfer problem. However, even with the overtraining, cat C-5 fell off markedly in performance with the practiced eye. Figure 1 shows day-to-day averages for two of the experimental animals, beginning at the stages when initial learning began to show up in their scores and carrying through until the criterion was met for learning during use of the second eye.

The experimental *S*s were markedly slower in learning the initial discrimination habits than the controls. For geometrical form discriminations the experimentals averaged 1550 trials in learning to the easier criterion; the controls averaged 235 trials. While the number of *S*s is small, only three in the former and four in the latter groups, the difference is so large as to warrant search for the variables that will account for it. The difference was smaller, but in the same direction for the brightness discrimination problem. Whether the control *S*s learned monocularly or binocularly seemed to make no significant difference in trials required, insofar as can be judged from our small numbers of *S*s. With adequate habituation to the hoods in the monocularly trained *S*s, no differences would be expected. The results provide a rough indication that there was no such disturbing effect.

During the pretraining period when the experimental cats were 14 to 17 (or to 20) weeks of age, and subsequently into the training period, they showed much evidence of visual unresponsiveness. The visual placing response did not appear, they seemed not to use vision to find food, and they bumped into objects. Locomotion was cautious until the animals had been in the play area (and later the experimental apparatus) repeatedly. They then became playful and moved about rapidly despite occasional headlong collision with walls or table legs.

Occasionally the masks loosened sufficiently to slip off the heads of the cats. Exposures of both eyes occurred in this manner for approximately 50 sec. a week, on the average. Despite daily experience of 30 to 90 min. with one eye uncovered and the other receiving diffuse light, more than two months (or some 30 to 70 hr. in light) were required before obstacles were avoided and food found by visual cues. By the time the first discrimination habit was learned, the numbers of hours of light exposure ranged from 38 for cat C-4 to 151 for cat B-2 (Table 2). Prior to solution, during the last one hundred trials or more, a characteristic change in the animals' manner of approach to

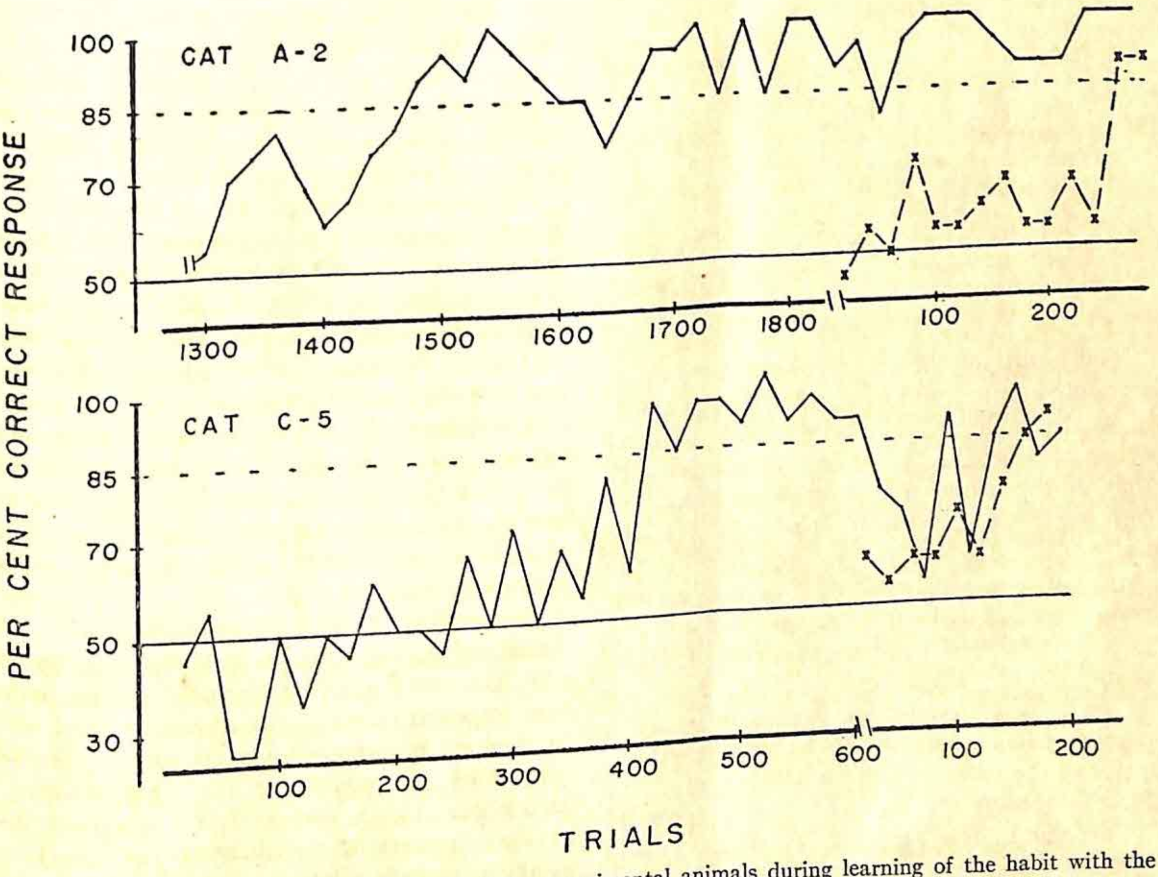

FIG. 1. Day-to-day performance by two of the experimental animals during learning of the habit with the original training eye open (solid line) and during the transfer test and learning with only the second eye open (broken line)

the stimulus doors gradually developed. Instead of proceeding directly into one or the other alley (or bumping into the partition between alleys), the animals would start into one alley, stop, sometimes continue, and sometimes back out and enter the opposite alley.

TABLE 2

Hours of Patterned Light Received in a Given Eye Prior to Learning to the Criterion Through That Eye

CAT	FIRST EYE	SECOND EYE
A-2	110	16
B-1	98	4
B-2	151	20
B-3	107	36
C-4	38	
C-5	64	18

DISCUSSION

The results of the transfer problem can be accounted for in terms of learning theory alone, if, in the naive animals, stimulation of either eye is considered as separate and unrelated to that of the other. *S–S* contiguity theory or *S–R* reinforcement theory could be invoked to "explain" the equivalence developed in the two eyes of the cats with previous binocular experience. Adult vertebrates, generally, which have been shown to give immediate transfer of monocularly trained habits (5, 7), probably do so partly because of previous extensive contiguous or immediately successive stimulation of the two eyes. Savings of learning time for the second eye in our naive cats would be accounted for, perhaps, by much general learning about the food-finding problem, the apparatus, and so forth, and by the extinction or reduction of ineffective modes of response. Space does not permit full discussion of the principles involved.

Alternatively, neuropsychological facts and theory may be drawn upon for a more complete search into the underlying mechanisms. Since the lateral geniculate nucleus of the cat shows lamination and absence of collaterals (10), the first and most obvious central nervous structure which would be expected to mediate equivalence of stimulation between the two eyes (where a learned habit is involved) is the occipital cortex. Just as in the higher primates, "... each hemi-cortex projects to the contralateral half-fields of both eyes, the line of division splitting the fixation point" (15, p. 1257), although the proportion of fibers decussating at the chiasm appears to be somewhat greater in the cat then in monkey or man (1, 9). Field theory (4) leads to the expectation that equivalence should be innately determined, since either eye would produce the same spatial pattern in the occipital cortex. The idea of separate cortical layers, closely superimposed but with insulation between them, could be used to give some degree of independence of action for each eye. The problem then to be faced by such theory would be to account for the elimination of this insulation in the experienced animal.

Hebb has challenged the position that equipotentiality, whether between different parts of the same retina or between the two retinae, must be innately given. He suggests (3, p. 45) that equipotentiality between the two eyes in the lower visual field of birds, and its absence in the upper visual field (6, 7) may be attributed to the relative use of these fields in pattern vision. The results of a recent experiment with doves (13) support this position. Hebb's schema can be applied to our results to indicate how activation of the same neural pathways might result from presentation of similar visual stimulation to either eye alone *after*, but not before, both eyes had previously been exposed to similar patterns many times. It is also conceivable, by recourse to the role played by eye movements in Hebb's schema, that repeated stimulation of the two eyes separately would result eventually in an activation of the same "phase sequences" from either eye. Alternation of monocular experience could provide the basis of later equivalence of stimulation. This possibility is now being tested on cats in our laboratory and on a chimpanzee at the Yerkes Laboratories of Primate Biology.

According to Hebb's schema, cell assemblies in and beyond the primary projection area of the cortex would be organized by the first learning in our experimental cats. The large reduction in numbers of trials taken for learning in the second eye would be expected if the linkage between cells in the primary projection area were all that was necessary. In view of the close juxtaposition of the primary projection fibers implied in the neurophysiological data (15) a fairly rapid linkage would be expected. Arrival of impulses at fibers in area 17 forming a spatial pattern closely adjacent to a similar group of fibers from the other eye which already had developed a "control" over more remote fibers (3, p. 72), would not be expected to result in a completely new sequence of firing. Rather, with repetition of such a pattern, the closely adjacent cells with their previously developed closed circuits would be increasingly apt to respond. The new stimulation would "take over" the previously developed phase sequences. Where the original habit was still very new, interference with it by stimulation of the second eye would be expected. We may tentatively ascribe the breakdown of the first habit in several of the experimental *S*s to this disruption of newly acquired firing paths and sequences upon first patterned stimulation of the second eye.

Results on the interocular transfer problem in fish (14) and birds (6), where transfer fails, and where vision is subcortically mediated and has little overlap in the two visual fields, show that the same stimulus to either eye independently may function as two distinct stimuli even in adult animals. In organisms having binocular vision, simple contiguity conditioning (*S–S* or *S–R*) will account for the development of either-eye-equivalence *if* the two eyes fixate in parallel. However, binocular coordinations are in themselves subject to improvement through use (11, 12), and such improvement is undoubtedly dependent upon innate neurophysiological mechanisms. Much work is still needed before the modes of interaction between these innate and experiential factors can be fully clarified. The relations between binocular use and habitual "suppression" of vision in one eye are only partially known. Perhaps our *S*s represent a special case of suppression or amblyopia. They may demonstrate the assertion by Linksz (8, p. 554) that the squinting child's eye "*stays* amblyopic, it does not 'develop' amblyopia."

The markedly slower learning of initial discrimination habits by the experimental group corresponds with similar findings in other species where early visual experience was restricted (3, 11, 13). The ultimate in improved rate of learning produced by previous learning is exemplified in Harlow's experiments (2). There is still the possibility that the prolonged learning periods shown by our cats may be due partly to impaired retinal and/or optic nerve function, since no one has yet determined what the required minimum daily exposure to light is for the prevention of atrophy or for the promotion of myelinization in the nerve. Still another alternative possibility is that the longer learning period involves a competition of visual learning with habits based on tactual-kinesthetic cues. That is, to speculate further, visual-association areas may have been encroached upon by tactual kinesthetically aroused "cell assemblies," so that their incorporation into the visual habit structures and sequences becomes more difficult than in the totally naive animal.

SUMMARY

1. Six cats were reared in darkness from birth to 14 weeks. They were then given diffuse light in one eye and patterned light in the other for 30 min. daily until the age of 17 or 20 weeks. Training of an initial visual discrimination habit in the open eye indicated a much slower learning than in control (normally reared) *S*s.

2. Transfer tests to the second eye showed immediate correct responses in the control *S*s, and failure (chance performance) of transfer in the experimental group. Learning of the habit in the second eye by the experimental group required about 20 per cent as many trials as the initial habit, or roughly the same number of trials as were required for the initial habit by the control *S*s.

3. Implications for theories of specific cell functions in learning and perception are discussed.

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ESTABLISHMENT OF A CONDITIONED DRIVE BASED ON THE HUNGER DRIVE

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A reinforcement theory of behavior assumes that a complete behavior cycle may be described as instigated by a motive, or drive, and terminated by a reward, or reinforcement. This notion is suggested in Figure 1, which depicts a motive-reward cycle; this is drawn to represent a gradually increasing motive, like the hunger drive, and its rapid reduction upon the presentation of a reward, like food.

This cycle can be divided into two phases: (*a*) the *motivating phase*, covering the period during which the drive is building up; and (*b*) the *reinforcing phase*, covering the period of the reward, during which the drive is falling off.

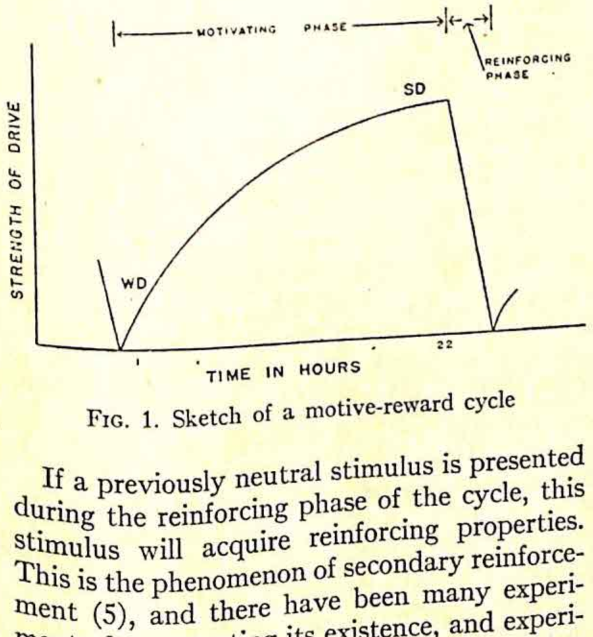

FIG. 1. Sketch of a motive-reward cycle

If a previously neutral stimulus is presented during the reinforcing phase of the cycle, this stimulus will acquire reinforcing properties. This is the phenomenon of secondary reinforcement (5), and there have been many experiments demonstrating its existence, and experimental inquiry into its empirical determining variables (2, 3) has begun.

Comparable investigations for the other phase of the cycle—the motivating phase—are fewer in number. Miller (7) has shown that a previously neutral stimulus presented during existence of a pain drive can acquire motivating properties. He used the term "fear" as a name for this secondary motive based on pain.

The present investigation was designed to determine whether a stimulus situation will acquire motivating properties if it is repeatedly presented during the motivating phase of the cycle shown in Figure 1. Strength of drive, in Figure 1, is relatively high at point *SD* and it is relatively low at point *WD*. Will a stimulus situation repeatedly presented at point *SD* acquire stronger secondary motivating properties than the same stimulus situation repeatedly presented at point *WD*?

METHOD

Subjects

Two groups of male albino rats, 12 rats per group, were the *S*s. These groups will be designated "SD" (for strong drive) and "WD" (for weak drive). The animals were procured from Albino Farms, Redbank, New Jersey, and were 80 to 100 days old at the beginning of the experiment. For one week prior to the beginning of the experiment, they were placed on a 24-hr. feeding schedule and each rat was handled twice daily.

Apparatus

Each rat in both groups was placed in a special stimulus situation, called the *striped box*, 30 min. each day for 24 consecutive days. The striped box was a triangular cage, the inner walls of which were painted in diagonal black-and-white stripes. On the triangular floor of the cage was mounted a wire "hurdle" 3 in. in height whose purpose was to attempt to increase the distinctiveness of the striped box as a stimulus situation.

Procedure

The animals of Group SD were placed in the striped box each day under conditions of strong hunger drive; these animals had been deprived of food for 22 hr. Group WD received its daily session in the striped box under conditions of relatively weak hunger drive; these animals had been deprived of food for only 1 hr. Both groups of animals received their daily rations in their home cages. Each rat was housed in a separate living cage and was given a daily ration of 25 gm. of a food mixture; the mixture was composed of 40 per cent ground Purina Dog Chow and 60 per cent water. Food consumption was measured, by determining the weight of food eaten from a food cup, twice during each daily feeding period—at the end of 5 min. and at the end of 15 min. During the course of the experiment the ration was supplemented by a small piece of lettuce given weekly.

In reference to the motive-reward cycle sketched in Figure 1, Group SD was placed in the striped box each day at approximately the level labeled *SD* on the curve.

Group WD was placed in the striped box at approximately the level labeled *WD*.

Immediately following these 24 training days, there were 2 test days, during which four test trials were made for each of the 24 animals. On each of these tests, each *S* was presented 50 gm. of the food mixture, in the striped box; for these tests, it was necessary to use more than 25 gm., inasmuch as all *S*s had eaten their 25-gm. daily ration in less than 15 min. during the pretesting procedure. Measures of eating were made after 5 min. and after 15 min. For each *S*, food was removed at the time of the 15-min. measure, and the food was not returned to the animal.

These tests were scheduled so that level of hunger drive would be intermediate between the two levels used in the "training" series; during the training series, the drive levels had been 22 hr. for Group SD, 1 hr. for Group WD. The first test trial was made 12 hr. after feeding on day 24, the second test trial 12 hr. later, and the third and fourth test trials at successive intervals of 12 hr. For each test trial, the *S*s remained in the striped boxes for 30 min.

From the end of each experimental session (pretesting sessions and testing sessions) until the beginning of the following session, water was available at all times in each *S*'s living cage.

This investigation had two replications. The experimental procedure was carried through for 12 of the 24 animals (6 in each group) during the months of July and August. A replication was made with 12 additional animals during the months of October and November.

RESULTS

During the test trials, the animals in Group SD consumed more food than did the animals in Group WD. Measures of food consumption were made at the end of the first 5 min., and at the end of the first 15 min. of each test trial. These two measures, for test trial 1 and for test trials 1 to 4 combined are presented in Table 1. An inspection of the table will reveal that Group SD was superior to Group WD for all of these measures. Furthermore, the results obtained in the two replications of the experiment are similar.

Measures of food consumption during the last four days (days 21 to 24) of the "training" series were used as indicators of voracity of individual rats, and the effects of this variable were "ruled out" by means of analysis of covariance. The results of one of these analyses—5-min. food consumption for test trials 1 to 4—are presented in Table 2. The other comparable analyses (15-min. food consumption for test trials 1 to 4; 5-min. food consumption for test trial 1; 15-min. food consumption for test trial 1) all yielded *F* ratios indicating significance at less than the .05 level. These analyses are not presented here.

Food-consumption means obtained during the testing procedure were adjusted for eating differences during the pretesting procedure. A method described by Snedecor (9) was used in making these adjustments. In Table 1, these adjusted means are presented, in parentheses, just below the corresponding actual means.

TABLE 1

Mean Food Consumption During Test Trials

	FOOD CONSUMPTION PERIOD (MIN.)	TEST TRIAL 1		TEST TRIALS 1–4 COMBINED	
		SD	WD	SD	WD
Replication 1	5	10.0 (9.9)[*]	8.1 (8.2)	46.5 (45.9)	35.7 (36.3)
	15	25.9 (25.4)	21.8 (22.3)	107.7 (106.4)	89.0 (90.3)
Replication 2	5	7.3 (8.0)	5.3 (4.6)	43.6 (45.9)	35.2 (32.8)
	15	20.2 (21.6)	19.0 (17.5)	102.5 (106.7)	97.3 (93.0)
Replications 1 and 2 combined	5	8.6 (8.7)	6.7 (6.6)	45.1 (45.4)	35.4 (35.1)
	15	23.1 (23.3)	20.4 (20.2)	105.1 (105.6)	93.2 (92.7)

[*] Figures enclosed in parentheses are adjusted means.

TABLE 2

Analysis of Covariance: 5-Min. Food-Consumption Test Trials 1–4

SOURCE OF VARIATION	ADJUSTED SUMS OF SQUARES	*df*	MEAN SQUARE	*F*	*p*
Adjusted group means (SD vs. WD)	615.63	1	615.63	23.52	.001
Within groups	523.66	20	26.18		
Total	1139.29	21			

DISCUSSION

The results of this experiment indicate that a neutral stimulus can acquire motivating properties if it has been associated with a primary drive state. How is this conditioned drive, or secondary drive, acquired? Two possibilities are suggested.

First, it is possible that reinforcement is necessary for the establishment of this conditioned drive, just as reinforcement is believed necessary for many other forms of learning. In his discussion of drive externalization, Anderson (1) suggested that an internally aroused drive which has been satisfied in a relatively constant external situation will become aroused by this external situation. A similar view has been recently stated by Hull (6), who has assumed that primary reinforcement, or the abrupt diminution in a drive, is necessary for the establishment of a secondary motive. In the present experiment, neither group received reward in the striped box, and there was no reward for some time after leaving the box. It is possible, however, to regard this experiment as a delayed-reward experiment. Group SD received food 1 hr. after its daily striped-box experience, and Group WD was fed 22 hr. after striped-box experience. Can the superiority of Group SD be attributed to this shorter interval of delay? On the basis of evidence from experiments by Wolfe (10) and Hamilton (4), it would appear that such long delays in reward are ineffective for learning in the rat. It would therefore seem unlikely that differences in delay of reinforcement could account for the differences obtained in this experiment.

Second, it is possible that a conditioned drive is a form of learning for which reinforcement is not necessary. If the hunger drive is considered a set of internal responses, then the conditioning of a hunger drive may be nothing more than the conditioning of these responses to new stimuli. Mowrer (8) has suggested that reinforcement is not necessary for the conditioning of smooth-muscle responses. If internal drive responses are similar to smooth-muscle responses in this respect, then reinforcement would not be essential for the establishment of a conditioned drive.

SUMMARY

Two groups of rats were placed in striped boxes 30 min. a day for 24 consecutive days. Group SD received this daily experience under conditions of 22-hr. food deprivation; for Group WD, the deprivation period was 1 hr. Following this procedure, the food consumption of each group was measured under 11½-hr. food deprivation. Group SD ate more food than Group WD. These results suggest that a previously neutral stimulus situation (the striped box) can acquire motivating properties from association with a relatively strong drive state. These results are interpreted to suggest that reinforcement is not essential for the establishment of a conditioned drive.

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EFFECT OF A SECONDARY REINFORCER ON CONSUMMATORY BEHAVIOR

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There have been many experimental demonstrations of secondary reinforcement and some of the conditions for its establishment have been investigated (1, 3, 6).

After it has been established, how does a secondary reinforcer operate? Does its operation yield the same sort of results as those produced by a primary reinforcer? One of the characteristics of a primary reinforcer is that it reduces a primary drive. Does the operation of a secondary reinforcer have a similar drive-reducing result?

In the present experiment, a neutral stimulus was first established as a secondary reinforcer by association with the primary reinforcement of eating. After its establishment, the effect of the secondary reinforcer on food consumption was determined. If the operation of the secondary reinforcer involves reduction of the hunger drive, it would be expected to curtail food consumption.

METHOD

Subjects

Three groups of male albino rats, 12 rats per group, were the *S*s. The animals were procured from Albino Farms, Redbank, New Jersey, and were 80 to 100 days of age at the beginning of the experiment. For one week prior to the beginning of the experiment, they were placed on a 24-hr. feeding schedule and each rat was handled twice daily.

Procedure

With the beginning of the experimental procedure, every animal in each group was fed a daily ration of 25 gm. of a food mixture consisting of 40 per cent ground Purina Dog Chow and 60 per cent water. Amount of food consumed was measured, by weighing, twice during each daily feeding period—at the end of 5 min. and at the end of 15 min. This procedure was repeated daily for 24 days. During the course of the experiment this ration was supplemented by a small piece of lettuce given weekly.

The three groups of animals will be designated Group "R" (for reinforcement) and Groups "C1" and "C2" (two control groups).

Group R. These animals received their daily food rations in a special cage, called the *striped box*; the inner walls of this cage were painted in diagonal black and white stripes. Each animal remained in the striped box for 30 min. each day. If uneaten food still remained at the end of the 30-min. period, this food was removed, with the animal, to its individual living cage.

Group C1. These animals received their daily food rations in their individual living cages. They received no striped-box experience. Each animal was removed from its living cage and handled twice during each daily experimental session.

Group C2. These animals were placed in the striped box for 30 min. each day for 24 consecutive days, but they were not fed in the striped box. They were given their daily food rations in their individual living cages. Their daily session in the striped box was begun 1 hr. after their feeding period.

Immediately following these 24 training days, there were two test days during which four test trials were made for each of the 36 animals. On each of these tests in the striped box each animal was presented 50 gm. of the food mixture; for these tests, it was necessary to use more than 25 gm., inasmuch as all animals had eaten their 25-gm. daily ration in less than 15 min. during the pretesting procedure. Measures of eating were made after 5 min. and after 15 min. For each animal, food was removed at the time of the 15-min. measure and the food was not returned to the animal. The first test trial was made 12 hr. after feeding on day 24, the second test trial 12 hr. later, and the third and fourth test trials at successive intervals of 12 hr.

From the end of each experimental session (pretesting sessions and test sessions) until the beginning of the following session, water was available at all times in each animal's living cage.

This experiment was done in two parts. First, the procedure was completed for 18 animals (6 in each group), and then a replication with 18 additional animals was made.

RESULTS

Group R did not consume *less* food than the control groups during the test trials in this experiment. Mean food consumption for each group is presented in Table 1.

Results of analyses of covariance, in which food consumption during the last four days (days 21 to 24) of the "training series" was used as the "adjusting" variable and 5-min. food consumption for test trials 1 to 4 combined was used as the "adjusted" variable, are presented in Tables 2 and 3.

Group R consumed *more* food than Group C2

TABLE 1

Mean Food Consumption during Test Trials

	FOOD CONSUMPTION PERIOD (MIN.)	TEST TRIAL 1			TEST TRIALS 1–4 COMBINED		
		R	C1	C2	R	C1	C2
Replication 1	5	8.9	9.2	8.1	39.2	44.0	35.7
	15	22.6	23.9	21.8	97.0	101.2	89.0
Replication 2	5	6.8	4.2	5.3	38.2	33.8	35.2
	15	19.8	16.1	19.0	98.0	91.5	97.3
Replications 1 and 2 Combined	5	7.8	6.7	6.7	38.7	38.9	35.4
	15	21.2	20.0	20.4	97.5	96.3	93.2

TABLE 2

Analysis of Covariance: 5-Min. Food Consumption Test Trials 1–4 Groups R and C2

SOURCE OF VARIATION	ADJUSTED SUMS OF SQUARES	*df*	MEAN SQUARE	*F*	*p*
Adjusted group means (R vs. C2)	154.39	1	154.39	9.25	.01
Within groups	333.94	20	16.697		
Total	488.33	21			

TABLE 3

Analysis of Covariance: 5-Min. Food Consumption Test Trials 1–4 Groups R and C1

SOURCE OF VARIATION	ADJUSTED SUMS OF SQUARES	*df*	MEAN SQUARE	*F*	*p*
Adjusted group means (R vs. C1)	1.81	1	1.81	0.15	> .50
Within groups	245.66	20	12.28		
Total	247.47	21			

TABLE 4

Probability Levels: Comparison of Food Consumption by Group R and Control Groups

MEASURE OF FOOD CONSUMPTION EMPLOYED	GROUPS R AND C1		GROUPS R AND C2	
	F	*p*	*F*	*p*
5 minutes Test trial 1	4.10	.10	7.56	.05
5 minutes Test trials 1–4	0.15	> .50	9.25	.01
15 minutes Test trial 1	1.86	.25	3.36	.10
15 minutes Test trials 1–4	0.55	.50	7.52	.05

[*] Probability values in this table were obtained from tables prepared by Merrington and Thompson (5).

during the eating test trials. The results of an analysis of covariance for these groups are shown in Table 2. Similar analyses were made for the other food-consumption measures obtained (15-min. food consumption for test trials 1 to 4; 5-min. food consumption for test trial 1; 15-min. food consumption for test trial 1). Group R was superior, in amount eaten, to Group C2 on all these measures. Probability levels were obtained for all measures by analysis of covariance, and these are presented in Table 4.

When Group R was compared with Group C1, such a consistent superiority for Group R was not found. Table 3 presents the results of an analysis of covariance for the 5-min. food-consumption measure for test trials 1 to 4 combined. For the first test trial only, however, Group R's food consumption was greater, and the difference approaches, but does not attain, the level conventionally required for statistical significance; this is true for both the 5-min. and 15-min. measures on test trial 1. These probabilities are reported in Table 4.

DISCUSSION

The major result of this experiment—that Group R did not consume *less* food than the control groups—suggests that a secondary reinforcer does not reduce a primary drive. This is in agreement with the results of a recent investigation by Simon, Wickens, Brown, and Pennock (7), who found that a secondary reinforcer which had been associated with drinking did not reduce the primary thirst drive.

This conclusion may be questioned by pointing out the possibility that the striped box may not have been established as a secondary reinforcer by the procedure followed in this experiment. This does not seem likely, however, inasmuch as the conditions said to be necessary and sufficient for the establishment of secondary reinforcement—the consistent and repeated association of a stimulus situation with primary reinforcement (4)—were repeated daily for 24 consecutive days. Secondary reinforcers established in much the same manner as described above have been found to serve as effective rewards for new learning (6, 8). They do not serve as drive reducers, according to the results of the present experiment and that of Simon, Wickens, Brown, and Pennock (7). The role of a secondary reinforcer, when it operates in learning, is much like that of a primary reinforcer, but its role in consummatory behavior appears to differ from the drive-reducing role of a primary reinforcer.

A minor result of the experiment is that Group R consumed *more* food than one of the control groups (C2). In an earlier experiment (2), it was found that a group of animals which received daily striped-box experience under a relatively weak hunger drive did not consume as much food in the test trials as another group for which the daily striped-box experience came under strong drive conditions. Group C2, in the present investigation, received the same weak-drive training conditions. It is possible that these relatively satiated animals were establishing a "conditioned satiation" in the striped box—that the striped box assumed satiating properties from its daily association with a state of satiation. Such an explanation would account for less eating in the test trials. This notion, however, does not explain the difference in drive-reducing properties between a "conditioned satiater" and a secondary reinforcer: Why should one reduce drive while the other does not?

Although it cannot be concluded definitely, the evidence suggests that Group R also consumed more food than the other control group (C1), for test trial 1 alone. It would seem likely that test trial 1 is a better measure than test trials 1 to 4 combined. At the time of test trial 1, all animals in all groups were alike with respect to (*a*) amount of food eaten daily for the 24 preceding days and (*b*) time since last feeding—12 hr. The groups differed only with respect to condition under which the 24-day daily feeding experience had occurred, and this was the experimental variable in this investigation. In the latter test trials (2, 3, and 4), the results may be obscured by the fact that all groups now have had eating experience in the striped box under hunger conditions which were presumably similar, and it might seem that any initial differences in the groups, existing at the time of test trial 1, would disappear.

From the results of this experiment, it seems that a secondary reinforcer does not reduce a primary hunger drive; there is suggestive evidence that it operates to increase the drive level. It is possible that a secondary reinforcer, which has previously been associated with food and eating, would acquire the property of stimulating appetite for food. The presentation of this "secondary reinforcer" would be expected to increase eating, rather than curtail it. This might describe the operation of a *conditioned appetite*. When food is presented to a hungry animal, it is not likely that sight of the food serves to reduce hunger drive, but, on the contrary, that it serves to increase hunger drive. Eating the food would be expected to reduce hunger, but seeing the food might be expected to increase hunger. Sight of food can be considered a secondary reinforcer; the secondary reinforcer used in this experiment, the striped box, might be expected to operate similarly.

The phenomenon of secondary reinforcement was probably given this name because of the discovery that it exerts an effect on learning similar to that of "primary reinforcement." They both facilitate learning. They seem to have opposite effects upon drive, however. A primary reinforcer has a "quieting" effect, while a secondary reinforcer seems to have an "arousing" or "energizing" effect by means of which drive is made stronger.

The superiority of Group R in this experiment might be interpreted in terms of conditioned appetite.

SUMMARY

A group of rats (Group R) was fed daily in a striped box in order to determine whether the striped box would acquire hunger-reducing properties. On later tests of eating in the striped box, Group R did not eat less than two control groups: C2 which had received daily striped-box experience without feeding there;

C1 which had received no striped-box experience.

These results suggest that a secondary reinforcer does not acquire the property of reducing a primary drive.

Two interpretations are suggested; these are called conditioned satiation and conditioned appetite.

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CUES FOR DISCRIMINATION AS SECONDARY REINFORCING AGENTS: A CONFIRMATION

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Recently there have been a number of fruitful researches attempting to establish the conditions and characteristics of secondary reinforcement. The present experiment represents a confirmation of one of the hypotheses developed from such research. Schoenfeld, Antonitis, and Bersh have concluded, in regard to secondary reinforcement, that "... selective reinforcement (i.e., discrimination training) is ordinarily required to yield a measurable effect" (3, p. 44). Other confirming data have been obtained by Dinsmoor (1), and a previous experiment by Williams could be directly interpreted in these terms (6). The present experiment represents a further confirmation of this hypothesis.

METHOD

Twenty animals were trained to respond to black or white curtains in a discrimination device. The apparatus used was a modification of that devised by Grice (2). In the Grice apparatus *S* emerges from a starting box and is faced with a black and a white alley with black and white curtains. The alleys extend directly in front of *S*. He may choose either alley. Either the black-curtain alley or the white-curtain alley choice is rewarded by food in a small cup about 12 in. from the curtain. The sides on which the black and white stimuli appear are alternated randomly. Retracing is not permitted.

In the present experiment one-half the *S*s were trained to a black curtain and one-half the *S*s were trained to a white curtain; the alleys and the goal box were gray. The food cup appeared only on the rewarded side. After an initial day of 10 trials, the *S*s were given 15 trials a day for 7 days. All *S*s used in the later tests learned the problem to a criterion of 14 correct choices in 15 daily trials. Two *S*s failed to learn and were discarded. One animal died.

On the last day of training, the animals were given 4 test trials in a T maze with black and white goal boxes. No food was present in either the white or the black goal boxes on these trials. The goal boxes were placed at right angles to the maze arms so that they could not be seen from the choice point. The goal box which was the same color as the *S*s' discrimination cue was placed on the opposite side of the *S*s' position preference as exhibited in the discrimination apparatus. If the cues of discrimination had developed a property of reinforcement, we could expect a tendency for the *S*s to go to the side of the goal box which was the same color as the discrimination cue, i.e., the animals that had previously been trained to black should now show a greater approach tendency to black goal boxes than to white goal boxes, on trials subsequent to the first trial, etc. The direction of the choices in the two groups supports this prediction. Sixteen of the last three trials (a total of 27 choices) in the animals trained to black during discrimination were to the black goal-box side; 13 of the 24 choices for the white-trained group were to the white side. A total of 58.8 per cent of the choices on the last three T-maze trials were to the goal box having the cue to which the animal had been trained. None of these differences, however, could be shown to be significantly different, and a further attempt to measure the secondary reinforcement was instituted. On the following day, after 10 "refresher" trials in the discrimination device, the *S*s were trained to go to one side or the other in the T maze. Half the *S*s found food in a goal box which was the *same* color as their discrimination color, i.e., if trained to go to white in the discrimination device, they found food in a white goal box. The other half of the *S*s found food in a goal box which was opposite in color to that which had been positively rewarded in the discrimination device. The groups were matched so that each of the subgroups had had an approximately equal number of trials to each side during the previous test period.

TABLE 1
Subgroup Means for the Training and Retraining Conditions

SIMILAR CUES	DISSIMILAR CUES
Discrimination black Goal box black 4.6 ($N = 5$)	Discrimination white Goal box black 6.25 ($N = 4$)
Discrimination white Goal box white 5.0 ($N = 4$)	Discrimination black Goal box white 9.8 ($N = 4$)

It should be expected that if a state of secondary reinforcement was evoked in the presence of the color cue, learning would be facilitated in the group which had to learn a response followed by this group's "secondary reinforcing" stimulus or cue. In such cases the *S*s would receive both primary and secondary reinforcement following the correct choices and no reinforcement for the incorrect choices. In contrast, the opposite-trained group would be slowed down in rate of learning by finding primary reinforcement on one side and secondary reinforcement on the opposite side.

RESULTS

The results, by subgroups, are given in Table 1. The groups in which the discrimination cue and the goal boxes were the same color learned more rapidly. An analysis of variance results in an F of 5.16 for the columns (similarity-dissimilarity variable). This is significant at between the 1 per cent and 5 per cent levels of confidence. The other F's were not significant.

CONCLUSIONS

The results indicate that stimuli which serve as discriminanda for primary reinforcement will acquire the property of reinforcement. Several unpublished experiments by the present authors fail to reveal demonstrable secondary reinforcing effects of neutral cues associated with reward when these cues did not serve as discriminanda for the reward, e.g., black and white goal boxes in T mazes. Similar results have been reported by Seeman and Kjenaas (4) and by Schoenfeld, Antonitis, and Bersh (3). It is conceivable that discrimination training in relation to the neutral cues is a necessary condition to "sensitize" the animal to such cues. Whether such a condition is facilitative or is necessary has not, however, been established.

The present data are supportive of the Spence-Grice statements in regard to secondary reinforcement and discrimination learning (2, 5). This interpretation has indicated a critical role of immediate secondary reinforcement in response to the discriminanda. Our data indicate that such secondary reinforcement is operative.

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THE EFFECTS OF HUNGER AND TYPE OF MANIPULANDUM ON SPONTANEOUS INSTRUMENTAL RESPONDING[1]

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Several studies have shown that spontaneous activity increases with hunger (4). However, little is known about the effect of drive on the spontaneous occurrence of a specific instrumental response. One purpose of this study was to determine the effect of hunger on spontaneous responding in a Skinner box situation.

The kind of manipulandum offered the animal may also influence spontaneous instrumental responding. Human subjects spontaneously respond more to a larger or brighter stimulus (1). Under some conditions, *spontaneous* responding in the Columbia Skinner box (5) is higher than *extinction* responding in the Yale apparatus (2, 3). Among other differences, the Yale apparatus has a much shorter bar. The second purpose of this study was to measure spontaneous responding with a short Yale bar, a long Columbia bar, and a chain in identical Yale-type boxes.

METHOD

Subjects and Apparatus

The *S*s were 103 male albino rats 90 to 110 days old. The apparatus consisted of three identical Skinner boxes of the type described by Ellson (2). Each was a 12-in. cubical compartment enclosed in a large shell packed with insulating material. A 7½-w. frosted light bulb was placed over the center of an observation window on top of each box. The interior was painted a uniform pewter gray. The compartment was ventilated by a gentle stream of compressed air and contained a water bottle near the front.

The short-bar box had a bar 2.17 in. long and ⅛ in. in diameter which was ½ in. in front of and parallel to the rear wall. The long-bar box had a bar 4.0 in. long and ⅛ in. in diameter in the same position. The chain box had a beaded lamp chain instead of a bar. The chain hung through a hole in the top of the box and swung freely ½ in. in front of the rear wall at the height of the bars in the other boxes. In all three boxes, the response mechanism required a force of 15 gm. for a complete depression.

Procedure

The rats were habituated and satiated by a procedure identical with that of Perin (3). Briefly, this was as follows: On days 1 to 7, the rats were fed wet mash in their home cages for ½ hr. a day. On days 8 and 9, they were only fed dry pellets for ½ hr. in the Skinner boxes each day. On day 10, 40 pellets were dropped one by one to the rats to achieve adaptation to the apparatus noises. On day 11 all rats were satiated for an hour on wet mash.

Half the animals were tested immediately after satiation with 17, 16, and 18 rats in the short-bar, long-bar, and chain boxes, respectively. The other half were tested 23 hr. after satiation with 18, 17, and 17 rats in the three boxes. During testing, the response mechanisms were in the boxes for the first time, and the number of responses in an hour was recorded. An analysis of variance showed that the six groups were homogeneous with respect to body weight, amount eaten at satiation, and time to consume the 40 pellets during habituation.

TABLE 1

The Mean Number of Spontaneous Instrumental Responses in an Hour for Two Levels of Hunger and Three Types of Manipulandum

HUNGER	MANIPULANDUM		
	Short Bar	Long Bar	Chain
Satiated	2.00	2.60	2.61
23 hours	2.38	21.18	23.00

RESULTS AND DISCUSSION

The results are shown in Table 1. At satiation responding is low in all three boxes. After 23 hr. of deprivation, the number of responses is reliably higher ($p < .01$) for both the long-bar box and the chain box but *not* for the short-bar box. At 23 hours responding in both the long-bar and chain boxes was reliably higher than in the short-bar box ($p < .01$). An above-below the median chi-square analysis was used since the data were not normally distributed nor were the variances equal. Measures of the number of responses and time before a 5-min. criterion gave similar results.

The effect of the larger bar and the movement provided by the chain may possibly be explained by stimulus intensity (1) interacting with drive to influence innate or previously learned behavior. However, the manipulandum properties, variation of which governs spontaneous response strength, cannot be specified from the present data. Nor can it be assumed that spontaneous instrumental responding is any simple function of hunger, for *whether* hunger will exert an effect seems itself contingent on the type of manipulandum.

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[1] This study is based on a master's thesis submitted to Duke University. The author wishes to express his gratitude to Dr. Sigmund Koch for his advice and aid throughout the study. The author also wishes to express his appreciation to Dr. Karl Zener for his encouragement and material support.

CONCLUSION

Spontaneous instrumental responding in the Skinner box is jointly dependent upon hunger and type of manipulandum.

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RESPONSE LATENCY AS A FUNCTION OF CHANGE IN DELAY OF REWARD[1]

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Early studies showed that performance in learning situations was a function both of amount (6) and delay (7, 19) of reward. It is natural that theorists should attempt to lump these two variables in a single treatment. Thus, Hull (9) made the limit of habit strength a positive growth function of amount of reward and a negative growth function of its delay. More recently (10), denoting these two functions as K and J, respectively, he entered them as multipliers of $_{S}H_{R}$ in determining reaction potential. Spence (17), in a recent modification of this view, suggested a single incentive-motivational factor, K, determined by amount and delay of reward. As he pointed out, however, there is much less evidence for the nonassociative character of delay than for that of amount.

Two problems are involved: (*a*) Assuming that incentive variation influences $_{S}H_{R}$, does it affect the upper limit or the rate of approach to that limit? (*b*) Assuming a constant rate of approach, is performance level determined by way of $_{S}H_{R}$ or directly through $_{S}E_{R}$?

Varying amount of reward, Crespi (1) and Zeaman (20) presented convincing answers to both questions. Growth curves fitted to their data (11, 20) had the same exponential constants but different asymptotes. When the asymptote had been reached, increase or decrease of reward produced a rapid shift to the performance level characteristic of the new amount, a result pointing to a direct effect of the variable on $_{S}E_{R}$. There was even evidence of a "contrast effect" not predicted by either of Hull's formulations.

Turning to delay of reward we find less certainty. Hull (11), who had already expressed doubt as to the relation between J and $_{S}H_{R}$ (10, p. 176, footnote 2), analyzed Perin's data on latency of bar pressing. Converting latencies to units of $_{S}E_{R}$, Hull showed that fitted growth curves varied both in asymptote and exponential constant as functions of delay of reinforcement. Frank, in an unpublished experiment (personal communication from Lewis B. Frank), trained hungry rats in a runway to a delayed food reward. He found that those *S*s that learned reached the same latency asymptote as a group with immediate reward but took longer to reach it.

A test of the second problem stated above is to change the delay of reinforcement after learning has taken place. Spence predicted that if habit was the mediating variable, response strength would not be reduced when delay was lengthened. If habit was not involved, however, reduction of response strength would be immediate.

Two studies from the Iowa laboratory were concerned with this problem. Harker (8) trained two groups of rats to press a bar with delays of 1 and 10 sec., respectively. After 40 trials he reversed delays for half of each group. Using latency reciprocals, he found that the group with decreased delay gained more than the 10-sec. controls but failed to overtake the 1-sec. controls. The group with increased delay continued to improve at a rate not significantly slower than that of the 1-sec. control group. Although these results are complicated by the fact that learning was still in progress, they point to the importance of a habit factor.

Logan (13) trained rats to touch either of two bars, one with a 5-sec. delay of reinforcement, the other with a 1-sec. delay. When he reversed delays for half the animals, their choices and response times gradually shifted until they reached those of the controls. In the light of Spence's predictions these results are equivocal. The loss of response strength with increased delay argues against the role of habit, the gradualness of that loss argues for it. As Logan pointed out, the rate of change may have been retarded in his study by stimulus generalization between the two bars.

In the present experiment delay of reinforcement was changed after improvement in the performance of a single response had reached a plateau. It should, therefore, provide needed supplementary evidence on which to base a decision between $_{S}H_{R}$ and $_{S}E_{R}$. Incidentally, we hoped to throw light on problem *a*, i.e., the

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question of how, if at all, delay of reward affects the course of initial learning.

METHOD

In choosing a response for this purpose, an important consideration is secondary reinforcement. In so far as the response produces a change in the external situation that lasts until reinforcement occurs, the effectiveness of delay is diminished. This was amply demonstrated in the T maze by the studies of Wolfe (19) and Perkins (15). A second restriction is imposed by the necessity of precise control of the time interval between response and reinforcement. On both counts the running response used by Crespi, Zeaman, Deese and Carpenter (2), and Frank in similar work was rejected. Logan's (13) discrimination method probably provides the best control of secondary reinforcement but introduces the generalization effects already mentioned. As a compromise between these requirements we resorted to the bar-pressing response used by Perin and Harker.

Four groups of rats, two experimental and two control, were trained to press a bar; in one E and one C group the response was rewarded by a pellet after 2.5 sec., in the other two groups after 10 sec. These two intervals were chosen to permit a possible contrast effect to appear. Response latencies were measured until each *S* reached an arbitrarily designated asymptote; experimental *S*s were then switched to the opposite delay while control *S*s were kept under the same conditions. Training continued until each *S* met the criterion of an "asymptote" a second time.

Apparatus[2]

The training situation was an unpainted wooden box with a wire floor. A vestibule 7 by 4 by 5½ in. and a main compartment 9 by 6 by 5½ in. were separated by a sliding transparent plastic door. Each part was lighted by a 6-w. lamp under a hinged roof of window screen painted white underneath. Darkening the room gave one-way vision of the interior. In the wall of the main compartment opposite the door, 1 in. up and to the left, was a horizontal slit through which the bar, a T-shaped piece of metal 2 in. across, could be inserted ⅝ in. and withdrawn. Just to the right of the bar an aperture 1¾ by 1½ in. was closed by a metal door pivoted at the top. When the door was released, it exposed a recess in which the pellet was placed.

Raising the vestibule door tripped a mercury switch and started two electric clocks, one recording seconds, the other hundredths of seconds. Depression of the bar by about 1 mm. stopped the clocks. At the same time it activated two Hunter decade interval timers (12) connected in parallel and set to give a .5-sec. impulse at the end of the desired period of delay. This impulse released the door to the food recess and simultaneously produced a sharp hum in the releasing relay.

Procedure

Adaptation. Animals were put on a 24-hr. feeding rhythm two to five days before the experiment began and kept on it thereafter. They were fed a Steenbock wet mash diet 30 to 40 min. at the end of a day's run. The pellets used as reward were "Little Friskies" dog food, selected to weigh close to 0.15 gm. each.

Adaptation took place in four steps, during which the bar was never presented:

Day 1. Each *S* was allowed two 5-min. periods to explore the box with doors open.

Day 2. Two dry runs of 5 min. each were given. *S* was started in the vestibule with doors closed and allowed to enter the main compartment. To accustom *S* to the noise of the releasing magnet, the food door was opened four times at 1-min. intervals.

Day 3. *S* was given four runs. On the first two runs *S* was permitted to eat five pellets scattered about a temporary paper floor. On the last two runs the paper floor was removed and *S* was allowed to secure five pellets, one at a time, through the open door of the food recess.

Days 4 to 6. To ensure uniform delay of reward, *S* had to be pretrained to get the pellet as soon as the door was opened. For this purpose the hum of the releasing mechanism served as a discriminative stimulus. Four runs a day were given; on each run *E* baited and released the food door five times. Pretraining covered at least three days, or 60 trials, and continued until *S* secured the pellet with a latency of less than 3 sec. on 15 out of 20 trials. *E* made a point of sounding the door release when *S* was in different positions, most frequently when *S*'s head was directed toward the location of the bar. Most rats completed this part in three days; a few took four to seven days.

Training. Next day the bar was presented for the first time and training was begun under conditions of delayed reinforcement. Three trials were given on the first day, four trials on the second and third days, and five trials a day thereafter. Trials were spaced, with most intervals falling between 10 and 20 min.

On each trial *S* was lowered into the vestibule with its head toward the rear wall. The door was raised as soon as *S* faced it and lowered after *S* passed through. Five minutes were allowed for pressing the bar; if no response occurred, *E* released the food door by a hand switch. When a response was made, *E* withdrew the bar as soon as *S* let it go. After *S* had eaten the pellet, it was returned to the living cage until the next trial. Starting with day 4, if a rat failed to respond on 10 trials, it was discarded.

Criterion of Learning

A critical feature of the method was the selection of a performance level at which to change the delay for the experimental *S*s. Such a criterion had to meet the following requirements: (*a*) Because of wide individual differences in learning rate it should be applicable to the scores of a single *S*. (*b*) It should be strict enough to approximate a final level. (*c*) It should be lenient enough to prevent large amounts of overtraining. (*d*) Since performance might shift up or down as a result of change in delay, the criterion should exclude a trend in either direction. (*e*) To reveal sharp subsequent fluctuations, it should specify an upper limit of variability as well as trend. (*f*) It should be simple to compute.

To meet these requirements, the following procedure was adopted: Every day each *S*'s median response latency was obtained. Calculations were based on even-numbered series of 6, 8, 10, or more consecutive daily medians. Means were computed for each half of the series ($\overline{X}_1$, $\overline{X}_2$) and for the whole series ($\overline{X}$). The *S* was held to have reached his asymptote when: (*a*) the absolute difference between $\overline{X}_1$, and $\overline{X}_2$ was not more than 0.2 $\overline{X}$; (*b*) $\overline{X}$ was not more than twice the smallest daily median of the series.

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[2] The writers are indebted to Mr. Slade Hulbert for building most of the apparatus.

The day after reaching this criterion each experimental *S* in the 2.5-sec. delay group was shifted to a 10-sec. delay; each member of group 10E was shifted to 2.5 sec.; groups 2.5C and 10C continued with the same delays as before. Training for each *S* was complete when it was again brought to the criterion.

A difficulty cropped up in the well-known variability of latency measures. After the data were collected, our working definition was found to need revision. In a few cases it proved to be too lenient; in a larger number, too severe. To arrive at a more satisfactory criterion, we plotted daily median latencies for each *S*. Using series of six to eight scores, we computed values for the three expressions given below at two points in each plot: the apparent asymptote and the "next best" preceding series. Each expression thus gave two frequency distributions. Cut-off points were then selected so as to lose as few cases as possible without including any "premature" asymptotes. The values finally chosen as a revised definition of *asymptote* for treating the results of this experiment were as follows:[3] (*a*)

$$\frac{|\overline{X}_1-\overline{X}_2|}{\overline{X}} < 0.25;\ (b)\ \frac{Range}{\overline{X}} < 1.3;\ (c)\ \overline{X} < 11 \text{ sec.}$$

Subjects

Fifty-seven hooded male rats, 3 to 5 mo. old, took part in the experiment. They were assigned to the four groups at random. One *S* was discarded for refusing to eat in pretraining, and 2 became ill. Four *S*s in the 2.5-sec. groups and 1 in the 10-sec. groups were dropped for persistent failure to press the bar within 5 min. Two *S*s in group 2.5E and 2 in group 10C failed to meet the working criterion of learning, either the first time or the second. Finally, 6 *S*s that completed the experiment failed to reach the revised asymptote, and their data were excluded. Of these 1 was in group 2.5E, 2 in 10E, and 3 in 10C. The results reported below are based on the remaining 39 *S*s.

RESULTS

Initial Training

Latency asymptote. Our first objective was to compare the final levels of performance reached under the two conditions of delay. Because the latency distributions were skewed, we first transformed the median latencies determining each *S*'s asymptote into logarithms. From these logs we computed individual means and from these, group means. Reconverted into antilogs, the group means appear in the left half of Table 1.

Since up to this point groups E and C had been treated alike, we are chiefly interested in the weighted means at the foot of columns 3 and 4, showing a criterion latency of 1.6 sec. for the shorter delay and 3.0 sec. for the longer one. A *t* test applied to the individual mean logs gave $t = 3.65$, $p < .01$.

Rate of learning. Our next question concerns the effect of delay of reward on rate of learning. As a first approach we counted the number of days it took each *S* to reach its asymptote. In counting we started with the day after the first bar response, omitted all days with no response, and excluded criterion days. Means were as follows: for the 2.5-sec. groups, 8.5 days; for the 10-sec. groups, 13.4 days. Since the distributions were somewhat skewed, a median test of significance was used (14). It yielded $\chi^2 = 4.27$, $p = .05$.

A longer time to reach the criterion implies a slower rate of learning. On the assumption that habit acquisition follows a growth function, a slower learning rate should be reflected in a smaller exponential constant. An attempt was made to test this inference on the present findings.[4] Owing to wide variation within groups in number of days to reach an asymptote, the data were broken down into several subgroups, and a separate curve was fitted for each one. The exponential equation proposed by Graham and Gagné (5) and adopted by Zeaman gave fairly satisfactory fits by the least-squares method, much better than the power function that was also tried (4). Values of C, the "growth constant," showed a regular decrease with increasing number of days to criterion. Similarly, its weighted mean value for all subgroups combined was greater for 2.5 than for 10-sec. delay. Since the restriction to small samples resulted in large errors of estimate and precluded tests of significance, the detailed results are omitted.

Change of Delay

Effect on final asymptote. Geometric mean latencies at the second criterion, computed by the same method as those at the first, are presented in columns 5 and 6 of Table 1. It can be seen that group 2.5E reached a final level close to that of 10C, while group 10E approximated that of 2.5C. A simple analysis of variance applied to the log latencies, however, gave $F = 1.24$, with $F = 2.87$ needed for significance at the .05 level. Little confidence, therefore, can be placed in the differences among these means.

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[3] One other rule was found necessary in establishing asymptotes; viz., a provision for excluding extremely deviant scores. Such a score was excluded if its distance from the next highest score was over half its distance from the lowest score in the series. For samples of six cases Dixon and Massey give 0.56 as the critical value of this ratio at the .05 level (3, pp. 146, 243).

[4] The mathematical aid given by Dr. Harold O. Gulliksen is gratefully acknowledged.

TABLE 1

Geometric Mean Latencies (In Seconds) at Criterion

GROUP	N	DELAYS TO 1ST CRITERION		DELAYS TO 2ND CRITERION		DIFFERENCE 2ND-1ST CRIT.	t
		2.5"	10"	2.5"	10"		
2.5E	11	1.6			2.9	1.3	3.07**
2.5C	11	1.6		1.9		0.3	0.95
10E	9		4.0	1.6		−2.4	3.98**
10C	8		2.1		2.6	0.5	1.20
Mean		1.6	3.0	1.8	2.8		

** $p < .01$.

Column 7 of Table 1 gives the mean differences between first- and second-criterion latencies in the four groups. The t's in the last column show that both the increase of latency for group 2.5E and the decrease for group 10E were significant at $p < .01$, while neither control group changed significantly. It is not surprising, therefore, that a simple analysis of variance of the log differences over all four groups gave $F = 9.9$, $p < .01$.

Table 2 presents t's for the mean log differences represented in column 7, Table 1. These ratios indicate that the shortening of response times brought about by reducing delay of reinforcement was reliably different from the change occurring in either control group. The effect of increasing delay, on the other hand, was not dependably greater than the effect of control conditions.

Duration of effect. As an indication of whether the effect was sudden or gradual, it is of interest to know how long it took the E and C groups to reach the second asymptote. A count was made of the number of days between the last criterion trial at the first asymptote—i.e., the point at which delay was changed for the E groups—and the first criterion trial at the second asymptote. The following means were obtained: for groups 2.5E and 2.5C, 7.9 and 2.7, respectively; for groups 10E and 10C, 4.4 and 3.2. Nonparametric tests (median and Wilcoxon's T [18]) applied to the difference between the 2.5-sec. groups failed to reach the .05 level of significance.

As in original training, it was hard to draw a single curve showing rate of change for all *S*s in a group because of wide variation in number of days to criterion. A line drawn, however, between those *S*s taking three days or less and those taking four or more divided all four groups roughly in half. By including the six scores making up the criterion, it was possible to plot mean latencies for six days in the first category and for 10 or 11 days in the second. These means were obtained, as before, by taking antilogs of mean log latencies.

The six-point curves showed no appreciable differences among the four groups. The longer curves, however, give some idea of how the change of delay exerted its effect in time. These appear in Figure 1. The curve for group 10E drops below its control in the first 3 to 4 days and remains below it thereafter. Group 2.5E shows an S-shaped rise. It may seem noteworthy that these two curves eventually reach the lowest and highest positions of the four. Since they represent only a fraction of the experimental groups, however, no generalization about contrast effect is warranted. The significant feature of both curves is the absence of

TABLE 2

Tests of Significance (t) of Differences between Groups in Mean Latency Shift from First to Second Criterion

GROUPS	GROUPS		
	2.5C	10E	10C
2.5E	1.50	5.15**	1.23
2.5C		3.77**	—
10E			3.72**

** $p < .01$.

any immediate response to the change of conditions. When a response did occur, it was gradual.

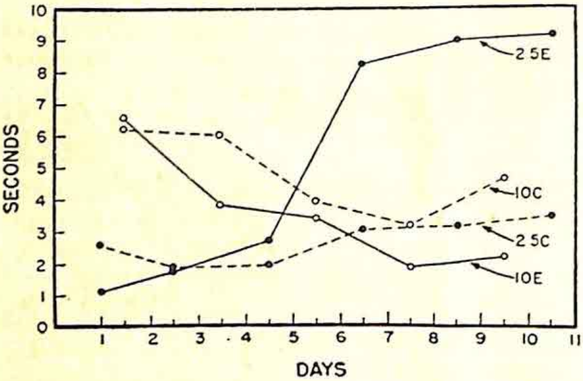

FIG. 1. Geometric mean latencies after change of delay for *S*s taking over three days to reach second asymptote. Curves smoothed by averaging successive pairs of means (except day 1 for 2.5-sec. groups). Each point represents *N* cases, as follows: group 2.5E, $N = 6$; 2.5C, $N = 4$; 10E, $N = 5$; 10C, $N = 4$.

DISCUSSION

One question asked in the context of Hull's earlier postulates was whether delay of reward affects the upper limit of habit strength or its rate of acquisition. Our results, together with Perin's in a similar situation, suggest an influence on both. Not only did our *S*s with a shorter delay approach their asymptote at a higher performance level than *S*s with a longer delay, but they tended to reach that level with less training. This finding fits the hypothesis that increasing delay of reinforcement leads to smaller increments of ${}_SH_R$.

A second question, raised by Hull's revised postulates, was whether delay of reward affects ${}_SE_R$ immediately or only indirectly through ${}_SH_R$. In Harker's experiment, it will be recalled, improvement was accelerated by reducing delay but was not retarded by increasing it. In the present study no change was made until improvement had at least temporarily ceased; under these conditions not only did reduction of delay lead to further improvement, but increase of delay produced some deterioration, although the latter effect was less pronounced. As Spence pointed out, such an outcome presents difficulties for an interpretation in terms of ${}_SH_R$. On the other hand, confirming Logan, we found that both effects took place slowly over a series of trials, implying an associative factor. Moreover, in the present study as distinct from Logan's, this finding could not be attributed to generalization between two manipulanda. It is clear that neither Hull's earlier postulates nor his later ones can account for these results without modification.

Spence (17) identifies K with the intensity of r_G, the anticipatory goal response, which in turn is determined by amount and delay of reward. Although he refers to K as nonassociative, he obviously means merely that it is independent of ${}_SH_R$, since r_G must be *learned* before it can enter ${}_SE_R$ (16). In so far as the results on delay of reward imply an effect on habit, it is suggested that the habit involved is the conditioning of r_G to present stimuli; not ${}_SH_R$ but ${}_SH_{r_G}$.

But in so far as the results imply a nonassociative factor, this interpretation merely shifts the problem from one habit to another. If habits do not lose strength, an increase in delay of reinforcement should weaken ${}_SH_{r_G}$ no more than ${}_SH_R$. To account for impaired performance we need another construct associated with delay of reward and parallel in function to *conditioned inhibition*. This process, provisionally denoted ${}_SI_{r_G}$, acts against ${}_SE_{r_G}$ just as ${}_SI_R$ opposes ${}_SE_R$. In nontechnical language it might be called *frustration*.

The present study provided much qualitative evidence for such a construct. Part of the variability of our latency measures seemed to be due to emotional behavior. Our animals frequently displayed marked hesitancy in approaching and pressing the bar. Once they had made the response, however, their behavior changed to a vigorous scraping, "weaving" back and forth between food door and bar position until the door was opened. An observer could hardly escape the impression that these animals were in conflict about responding to the bar. To establish the relation of this behavior to delay of reward, however, it would have to be shown to occur more frequently to long delays than to short ones. Unfortunately no such count was made.[5]

Another problem faced by Spence's r_G hypothesis is to explain the different results obtained by changing amount of reward and changing delay. In the first case the effect appears after one trial and is complete or even exaggerated (1, 20); in the second it builds up gradually. If strength of r_G can be changed in one trial by altering amount of reward, why should the same not be true of delay?

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[5] A complicating factor that may have caused conflict aside from delay-frustration was the rapid withdrawal of the bar, which sometimes seemed to startle the animal and even, on a few occasions, caught a paw.

An answer may be found in the relative difficulty of discrimination in the two cases. When reinforcement conditions are changed, a discrimination must be made, not between two stimulus objects as in Logan's study, but between an earlier and a later set of conditions. We suggest that the rate of adjustment will be a function of the discriminability of the change. According to this view there was less "before-after" generalization in Crespi's and Zeaman's experiments than in those varying delay of reward. Harker used delays of 1 and 10 sec.; Logan, 1 and 5; we used 2.5 and 10. It would be interesting to try making the shorter delay as close to zero as possible. Conversely, smaller differences in amount of reward should make for slower shifts in performance.

SUMMARY

Four groups of rats were trained to press a bar under two delays of reward, 2.5 and 10 sec., with an experimental and a control group at each delay. An "asymptote" was defined, based on median daily response latencies of an individual *S*. On reaching this criterion experimental *S*s were shifted to the other delay, while control *S*s were kept under the same condition; training continued until the asymptote was reached again.

Results were as follows:

1. At the end of initial training, response latencies with 10-sec. delay of reward were significantly longer than with 2.5-sec. delay.
2. The 10-sec. delay groups took longer to reach the first asymptote than the 2.5-sec. delay groups.
3. Reduction of delay from 10 to 2.5 sec. led to shorter latencies at the second asymptote. Increase of delay from 2.5 to 10 sec. resulted in longer latencies. Only the former effect was significantly different from the controls.
4. The changes resulting from both increase and decrease of delay were gradual.

These results were considered in relation to theories of the mechanism of delay of reinforcement.

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ON THE SELECTIVE REINFORCEMENT OF SPACED RESPONSES

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A standard procedure, originated by D. M. Page and used in the Columbia laboratory for establishing a discriminative response in the white rat, is one in which the positive stimulus (the S^D) is presented after a period of no responding in the absence of this stimulus (S^Δ). Thus, when the S^D appears and the rat responds, as by pressing a bar, it is reinforced with a pellet of food, after which S^Δ is presented. The S^D is again presented following a period (say 30 sec.) in which no responses during S^Δ have appeared. Any response during S^Δ serves to postpone the presentation of S^D for another 30 sec. The extinction of S^Δ responding, essential to forming a discrimination, is accordingly compressed within the early minutes of training, and good discriminations (involving very few responses during S^Δ and low latencies to the S^D) are rapidly established.

A similar procedure of reinforcement may be used when no specific discriminative stimuli are presented. In such a case, reinforcement is contingent upon a response that follows a period of nonresponse. For example, a bar press is reinforced only if it follows the preceding bar press by at least 30 sec.

Skinner (3, p. 306) used such a technique in a successful attempt to break down high rates of responding that had previously been set up under periodic reinforcement. However, more information from animals with no previous conditioning history is desirable. The present study was undertaken to determine (*a*) whether the strength of a conditioned operant (bar pressing) may be maintained under such a reinforcing schedule, (*b*) what changes in rate, if any, may be expected when the delay intervals are progressively increased, and (*c*) the nature of extinction following such a procedure.

METHOD

Three male albino rats of Wistar strain, approximately five months old, were used. Prior to and during experimentation, they were housed in individual living-working cages (2) and fed daily after 22½ hr. of food deprivation. Purina Laboratory Chow Checkers made up the basic diet, and the same food, in the form of 1-gr. pellets, was used to reinforce the bar-pressing response.

During experimental sessions, which were 1 hr. long, the living-working cages were placed inside separate lightproof, sound-resistant cubicles, which also contained the lever and the automatic food magazine. The animals were observed by means of a mirror placed over the cage and glass windows which replaced the lightproof doors. Illumination within the cubicle was provided by a 9-w. General Electric red lamp mounted 11 in. from the top of the cage. Previous work had shown this light to be nonaversive. The experimental room itself was dark.

The recording apparatus, the lever, and the food magazine were modified forms of those described elsewhere (see 2). The bar portion of the lever was ⅜ in. in diameter. It required approximately 10 gm. of force for depression and moved through a vertical distance of 14 mm. Since there were slight differences in lever operation, care was taken to see that each animal used the same apparatus throughout the experiment. The food magazine was made to discharge pellets rather than ground food. Cumulative kymograph records of responses to the bar, as well as polygraph records of the responses and the reinforcements, were made.

Reinforcement was accomplished by means of a timer and relay circuit which permitted the proper responses to operate the magazine solenoid. This apparatus was in the experimental room but not in the cubicles with the animals. The relay noises were audible within the cubicles; however, they presented no regular discriminative stimuli.

An outline of the experimental procedure is given below:

1. Six days of feeding regimen during which Lab. Chow was present for 1½ hr. followed by 22½ hr. of deprivation.
2. Seven daily 1-hr. periods of unconditioned bar-pressing rate determinations (operant-level determinations) followed by the regular feeding periods.
3. One day of conditioning with 30 regular reinforcements.
4. Thirty days, 1 hr. daily, during which reinforcement was contingent upon the following delay periods: 10 sec., 5 days; 15 sec., 6 days; 20 sec., 6 days; 25 sec., 6 days; 30 sec., 7 days.
5. Five daily 1-hr. periods of extinction, during which no bar presses were reinforced.

Experimentation was conducted at the same hour on consecutive days after the feeding regimen had been established. At the beginning of each experimental period, when the rats had been deprived of food for 21½ hr., the cages were placed within the cubicles, the levers were inserted, and the doors were closed. During the 30 days of training the first bar press on each day was reinforced with a pellet of food, and, thereafter, all responses were recorded but reinforcement was given only when a response came after a specified delay interval.

The data on unconditioned rate of bar pressing are not germane to the basic experimental questions of this study, but were collected for the sake of later comparisons. The 30 regular reinforcements were given to provide an estimate of the interval between responses to be used as our smallest delay interval. A previous study with three animals had already shown that bar pressing may be conditioned when, from the beginning, reinforcement is contingent upon a 30-sec. delay interval.

RESULTS AND DISCUSSION

From Figure 1, the median number of responses emitted by the three animals during each experimental hour of the delay training, one sees two findings. First, during the 10-sec. delay interval there is an orderly day-to-day decrease in the number of responses. This drop probably reflects the acquisition of collateral behavior to be discussed later. Second, as the animals are advanced to each new delay interval, the drop in the number of responses occurs during the first hour, and the number remains fairly constant throughout training at that interval. The greatest absolute difference in rate at any interval—between days 8 and 10—represents a difference of less than two responses per minute. Whether or not the rate would continue to drop with prolonged training at a given interval is not answered by this study.

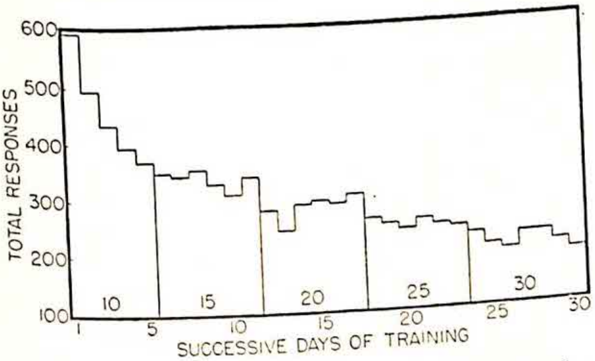

FIG. 1. Total number of bar presses emitted during each day of delay training. Each value represents the median value obtained from three animals. The numbers between vertical lines indicate the delay interval prevailing.

Figure 2 presents the relation between rate of responding and the delay intervals. The values have been derived from Figure 1 by dividing the number of responses during the last hour at each interval by 60 min. The linear curve, with a slope of −0.17, was fitted by the method of averages. Over the delay intervals used, the curve describes the rate function reasonably well.

Before considering the rest of the data, it will be helpful to analyze the reinforcing contingency that prevails. A response is never reinforced if it immediately follows a response; thus, a high rate of responding cannot be strengthened. Reinforcement of a single bar press serves to strengthen the response, but reinforcement will occur again only when the immediate strength (represented by the rate) has dropped to a rate during which responses are separated by an interval equal to or greater than the delay interval. This change in the rate of the conditioned response results from the partial extinction of bar pressing and the strengthening of behavior that is incompatible with it.

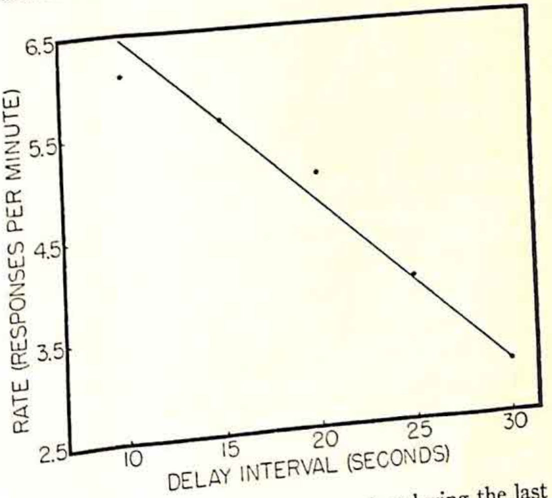

FIG. 2. Average rate of bar pressing during the last hour of delay training when the reinforcing contingency is increased by 5-sec. intervals from 10 through 30 sec. Values were obtained by dividing the number of responses on days 5, 11, 17, 23, and 30 in Fig. 1 by 60 min.

That many bar presses go unreinforced may be seen by comparing the number of reinforcements shown in Figure 4 with the number of responses on the corresponding days in Figure 1. In Figure 3 it is seen that the median time interval between responses, the *R–R* interval, is relatively small compared with the delay interval prevailing. (These values were taken from frequency distributions of the *R–R* intervals during the last hour at each delay interval.) The increases in *R–R* intervals with increases in delay intervals are regular but relatively slow. This is probably due to the fact that the effects of extinction are not reflected in the bar-pressing behavior as quickly as are those of conditioning. The decrease in the number of reinforcements at the higher intervals (Fig. 4) is much more rapid than the increase in the *R–R* intervals. Thus far, the data show that even though reinforcement does not occur for rates which exceed those dictated by the delay intervals, the rate of responding is considerably greater than that which would yield the maximum number of reinforcements, and that many responses go unreinforced before the strength is low enough to permit another reinforcement.

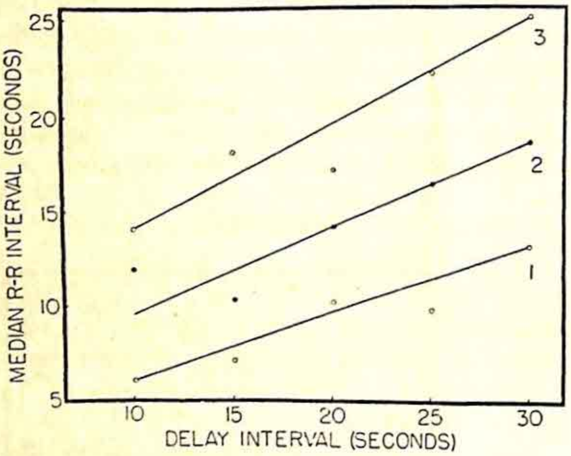

FIG. 3. Median *R-R* intervals for each animal during the last hour at each delay interval. Times were measured from the end of one bar press to the beginning of the next. The points for rats no. 2 and no. 3 have been displaced 5 sec. upward on the ordinate.

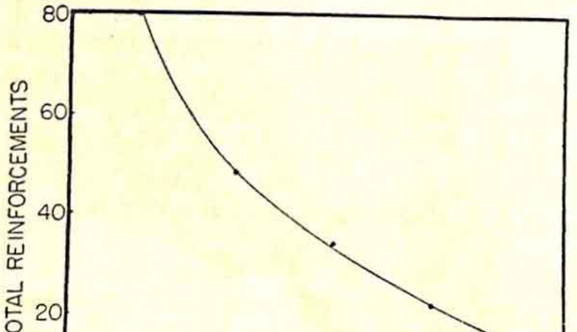

FIG. 4. Total reinforcements during the last hour of training at each delay interval. Each point is a median value obtained from three animals.

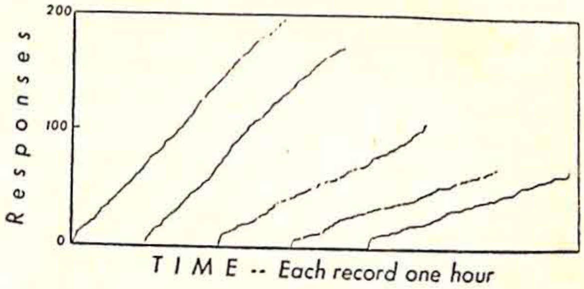

FIG. 5. Cumulative bar-pressing curves for rat no. 2 during 5 hr. of extinction

As Estes (1) has pointed out, in the free-responding situation the sum total of the probabilities of individual responses' occurring must equal unity. This statement implies that the organism must be doing *something* at all times, and that if the probability of one response decreases, that of incompatible responses must increase so that the sum of the probabilities is one. Applied to the experimental situation we are considering, this means that following reinforcement, bar pressing has a relatively high probability of occurrence and, as indicated previously, a number of extinction responses are emitted. Since none of these responses is reinforced, the immediate strength of bar pressing (and, hence, the probability of its occurrence) drops, and the animal emits behavior which has gained precedence. In the apparatus used, this behavior may be grooming, going to the water bottle, going to the food-cup slot in the rear of the cage, or climbing on the back of the cage. If this behavior occupies a temporal span greater than the delay interval necessary for reinforcement, a bar press following this chain is reinforced. This reinforcement serves to strengthen not only bar pressing but also that collateral behavior which *preceded* the bar press. Thus, when bar pressing has been weakened by extinction, the collateral behavior which has preceded prior reinforced bar presses has a slight differential in strength over other possible behaviors and, if it occurs and occupies enough time, it will be followed by a reinforced bar press. The strength of this collateral behavior is maintained through conditioned reinforcers provided by the stimulation attending the responses which make up a crude chain of behavior.

Although no quantitative records were made of the behavior which occurred between bar presses, in the case of each animal there developed an easily recognizable and predictable form of collateral response. Since this behavior was not specified in the reinforcing contingency, it was not surprising to observe that it was different for each animal. Between bar presses the animals emitted the following chains of behavior: Rat no. 1 went to the water bottle, poked its nose through the food-cup opening, returned to the water bottle, and returned to the bar. Rat no. 2 turned away from the bar and groomed, poked its nose through the food-cup slot, and returned to the bar. Rat no. 3 went to the water bottle and climbed on it, climbed the ventilation holes in the rear of the cage, poked its nose at the glass cover over the cage, and returned to the bar. Such factors as the number of paw licks, the number of trips between the food-cup slot and the water bottle, and the number of entries into and withdrawals from the food-cup opening contributed to the temporal spans of the chains. With the increase in delay intervals, more links were conditioned to the chain of collateral behavior. The relatively slow increase in the *R–R* intervals, pointed out above, may reflect the fact that the acquisition of these units further removed from the reinforced bar press becomes increasingly more difficult. A further study is planned in which measures of the acquisition and maintenance of this collateral behavior will be attempted.

During extinction, in which no bar presses were reinforced, there is an orderly drop in the rate of bar pressing. The data in Figure 5, which are the actual kymograph records for one animal and are representative of those for all, resemble extinction data obtained following intermittent reinforcement and contain none of the emotional bursts found in extinction curves following regular reinforcement. Since the procedure of reinforcement does not permit the conditioning of high rates or patterns of bar pressing, it is felt that the technique may be used in isolating those factors which are responsible for the characteristically different behavior following intermittent and regular reinforcement. At present there are no intermittent reinforcement data with which the number of extinction responses obtained in this study may be compared.

SUMMARY

1. Three albino rats, after preliminary training in the Columbia Skinner box, were reinforced with food pellets for bar presses separated from the previous bar press by progressively longer delay intervals, viz., 10, 15, 20, 25, and 30 sec.

2. As the delay intervals increase, (*a*) the rate of bar pressing decreases in a linear fashion over the range of intervals used, (*b*) the median time between successive responses increases slowly for each animal, and (*c*) the number of reinforcements decreases fairly rapidly.

3. Each animal developed clearly defined collateral behavior during the intervals between successive responses.

4. Extinction following such a reinforcement procedure resembles, in a qualitative fashion, that following intermittent reinforcement.

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AN EXPERIMENTAL INVESTIGATION OF EXTINCTION AS A MEASURE OF RETENTION[1]

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The phrase "resistance to experimental extinction" appears often in the literature of learning experiments, especially in connection with the theoretical systems of Hull (3) and Skinner (5), with an implication that the amount of resistance to extinction is a measure of retention of learning, a measure of "habit strength," or a measure of "reflex reserve." That concept is the subject of the present study.

The experiment was designed to investigate the role of experimental extinction as a measure of retention. The procedure is designed to compare experimental extinction measures with relearning scores after certain intervals of time, under normal conditions and under conditions designed to produce retroactive inhibition. We shall attempt to throw light upon the following matters: (*a*) What is the effect of extinction upon retention, as measured by relearning scores, in comparison to control groups? (*b*) How do relearning scores of extinction and control groups, cited above, compare with relearning scores of groups which have undergone training on an interpolated problem? (*c*) What effect does learning of a second problem have on the extinction scores of the first problem? (*d*) To what degree are the extinction curves congruent with the relearning curves in indicating that they are measuring the same thing: retention or habit strength?

METHOD

Subjects and Apparatus

The *S*s of this experiment were 244 naive rats, bred at Washington University.

There were two principal pieces of apparatus, a modified Skinner box, and a single-unit T maze. The Skinner box contained a buzzer and a retractable lever. An electrical timing device automatically advanced the lever, at 55-sec. intervals, through a slot into the Skinner box. As the lever entered the box, the buzzer sounded for approximately 1 sec. The lever remained within reach of the animal for approximately 10 sec. If the animal would press the lever within that time, a pellet of food was automatically delivered into the food tray, to the right of the lever. A 55-sec. interval would then elapse before the lever entered the box again. Pressing the bar produced an incidental audible click. A minimum pressure of about 8 gm. sufficed to trip the lever and deliver a food pellet. The device did not deliver more than one pellet of food during any single bar presentation, as it was desired that the animal should, after pressing the lever, eat the pellet before pressing the lever again. If, after the animal ate the pellet, it would press the bar again, *E* delivered an additional pellet manually through the tube leading into the food tray.

The wooden side of the box which was *opposite* the side where the food tray was situated (and opposite the side where the lever intermittently appeared) was constructed to be manually manipulated in a vertical direction. It served as the entrance to the maze.

Procedure

Preliminary training. Each animal was placed in the Skinner box about 10 min. per day for five successive days, where it was fed both from the food tray and from the lever fixed in a stationary position, in order to accustom the animal to the situation.

Learning of problem A. After preliminary training, all animals were trained on the Skinner-box problem. On the first day, a thin layer of grated cheese was spread on the lever in order to help overcome startle and fear induced by the sound of the buzzer. Thereafter, cheese was not used. Each animal was given ten trials (bar presentations) per day. The criterion for learning of the problem was at least one bar pressing on each of ten consecutive bar presentations, not necessarily on any one day. The drives varied randomly between 20 and 24 hr. without food. Trials were run on successive days. After each rat had learned this problem, it was placed in one of the 12 experimental groups. This selection was a random one insofar as sex and fur color were concerned. The remainder of the selection process was based upon an attempt to equate all 12 groups as closely as possible with respect to averages and variability in the following factors: number of trials until the criterion was reached, number of reinforced bar pressings occurring until the criterion was reached, hours of hunger drive, and age of the animal at the start of the experiment. A minimum of 20 rats was placed in each group. The schedule of the total procedure is listed in Table 1.

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[1] This article is based upon part of a dissertation submitted to the Graduate School of Arts and Sciences, Washington University, in partial fulfillment of the requirements for the Ph.D. degree. The writer wishes to express his sincere appreciation to Dr. Marion E. Bunch for his invaluable assistance throughout the course of this investigation.

[2] Now at Reed College.

It may be noted that we should be able to isolate three main variables, and to study their effects upon retention of problem A: passage of time (three different intervals after learning of problem A) during which the rats lived a normal cage existence, the effect of interpolated learning of the T maze, and the effect of experimental extinction of problem A.

Learning of problem B. One-half the animals underwent training in the T maze, beginning the day after they met the criterion on problem A, and continuing for a total of 6 successive days. In this phase of the experiment, the lever was prevented from entering the Skinner box, by separation of the electrical apparatus from the Skinner box itself. The motor was left running, however, so that the buzzer would sound periodically as in the original problem. The rats were placed in the Skinner box, and when the buzzer sounded, *E* lifted the door previously described, to permit entry of the rats into the maze. Half of the rats learned to turn right at the choice point, and half learned to turn left. Food pellets like those used in the Skinner box were used as reward in the maze. Each rat was given 15 trials per day on six successive days, a total of 90 trials. Then the training was stopped. This provided a uniform period of interpolated training and also approximately equal numbers of rewarded trials in the maze for the various groups concerned.

TABLE 1

Schedule of Procedures

GROUP	ORIGINAL PROBLEM	INTERPOLATED PROBLEM	RETENTION TESTS: (AFTER)		
			1 week	6 weeks	11 weeks
1	A		Relearn A		
2	A		Extinguish A	Relearn A	
3	A	B	Relearn A		
4	A	B	Extinguish A	Relearn A	
5	A			Relearn A	
6	A			Extinguish A	Relearn A
7	A	B		Relearn A	
8	A	B		Extinguish A	Relearn A
9	A				Relearn A
10	A				Extinguish A
11	A	B			Relearn A
12	A	B			Extinguish A

Extinction of problem A. During this phase of the problem, the buzzer sounded, the lever entered the Skinner box as in problem A, but food reward was not given. The criterion for extinction was a failure to press the lever at least once during ten successive bar presentations—not necessarily in the trials of any one day.

Relearning of problem A. The criterion was the same as in the original learning of the problem—pressing of the bar at least once during each of ten successive bar presentations, not necessarily in the trials of any one day.

RESULTS

For purposes of brevity we omit a table which indicates to what extent we have succeeded in equating the 12 groups at the completion of learning problem A. However, each group learned the problem with an average of about 60 trials, during which the animals received an average of about 31 reinforcements under a drive which averaged about 21.75 hr. The average age of the animals at the start of the problem was about 110 days. The means and standard deviations of these factors were not significantly different.

Table 2 lists the results of the extinction procedure, and Figure 1 lists part of these results graphically. With respect to trials to criterion, there are no significant differenecs between means or standard deviations. However, a striking trend of scores is noted; in every case, the groups which underwent interpolated training (groups 4, 8, and 12) on the maze required more trials to extinguish the original problem than did their control groups. For total bar pressings we again find no significant differences between means. The standard deviations of groups 6 and 8 are significantly different at the 2 per cent level of confidence. Groups which had interpolated

TABLE 2

Extinction Scores

GROUP	INTERVAL BETWEEN LEARNING & EXTINCTION	NO. RATS	TRIALS TO CRITERION		TOTAL BAR PRESSINGS		AGGRESSIVE BAR PRESSINGS
			Mean	*SD*	Mean	*SD*	Total
2	1 week	20	183.45	119.01	141.45	118.44	232
4	1 week	20	205.75	109.66	160.05	129.32	242
6	6 weeks	20	158.60	135.46	142.80	152.65	212
8	6 weeks	21	178.10	124.10	110.43	79.52	179
10	11 weeks	21	121.95	113.33	81.00	102.17	72
12	11 weeks	20	140.45	109.85	94.60	100.80	166

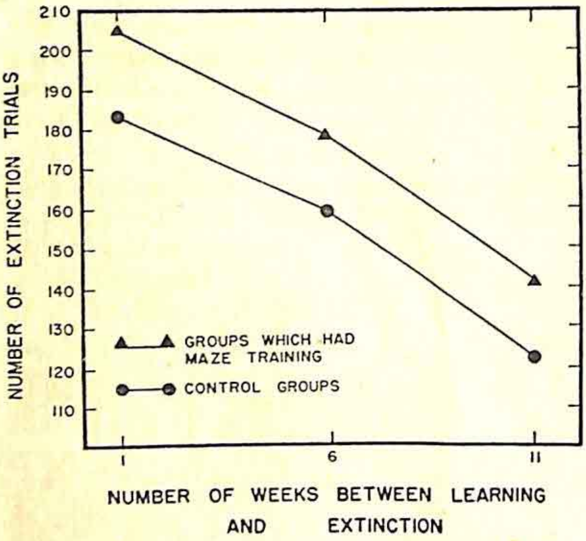

FIG. 1. A curve of resistance to extinction, drawn through the means of the groups

maze training pressed the bar more often during extinction than did groups which did not have such training in two of the three comparisons which can be made. "Aggressive bar pressings" refers to a type of response found only in the extinction procedure. It consisted of biting the bar, engaging in a tug-of-war with it, jumping on the bar, etc. Averages were not computed for this type of response because of the variability of the number of rats which engaged in such behavior. In two of the three comparisons which can be made, groups which underwent interpolated maze training showed more aggressive responses during extinction than did groups which did not have such interpolated training.

Table 3 lists the results of the relearning procedure, and Figure 2 is a graphic illustration of part of these results.

TABLE 3

Relearning Scores

GROUP	EXT. A	RELEARN A	TRIALS TO RELEARN		BAR PRESSINGS (REWARDED)		SAVINGS SCORES	% OF NON-BAR-PRESSING TRIALS ON WHICH ANTICIPATORY MAZE-ENTRY RESPONSES OCCURRED
			Mean	*SD*	Mean	*SD*	% saved	
1		1 wk.	15.75	8.23	17.30	8.13	73.9	
2	1 wk.	6 wk.	27.30	15.14	20.50	6.41	55.1	
3		1 wk.	15.55	6.61	23.30	7.00	74.1	83.0
4	1 wk.	6 wk.	22.70	11.96	21.00	8.10	62.0	45.4
5		6 wk.	24.15	11.56	23.00	8.49	60.1	
6	6 wk.	11 wk.	24.20	14.66	20.20	8.48	59.8	
7		6 wk.	26.05	11.58	23.64	7.85	57.6	69.0
8	6 wk.	11 wk.	24.19	13.49	20.57	7.30	59.8	41.1
9		11 wk.	25.00	13.49	20.50	8.26	58.0	
11		11 wk.	25.75	11.68	20.45	6.61	57.4	66.3

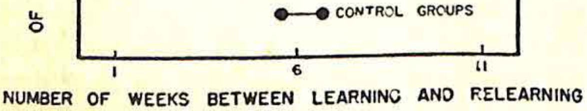

FIG. 2. Relearning curves of nonextinguished groups, drawn through means of groups

In comparing relearning scores among the various groups, we find the only significant differences are those correlated with the time variable. The means of groups 1 and 5 and of groups 1 and 9 are significantly different at the 2 per cent level of confidence. Groups 3 and 11, both of which had maze training, are significantly different at the 1 per cent level of confidence. The standard deviations are not significantly different.

In comparing bar pressings during relearning, we find that the only significant difference along the time dimension is between groups

1 and 5, at the 5 per cent level of confidence. The variable of interpolated learning has produced only one significant difference, between groups 1 and 3, at the 2 per cent level of confidence. The variable of extinction has produced no significant differences between means. There are no significant differences between standard deviations.

The last column of Table 3 indicates, in percentage terms, how often during the relearning trials the maze-trained rats made futile anticipatory maze-entry responses on trials not involving bar pressings. Such responses consisted generally of scratching and pawing at the gateway to the maze, but less frequently they included climbing, exploring, and the like. Data for such maze-entry responses among control groups were not recorded because they rarely occurred.

DISCUSSION

In general, experiments show that the number of trials required to relearn a task increases with increasing time intervals between learning and relearning. By the same token, it may be assumed, if one is to regard extinction scores as measures of habit strength, that decreasing numbers of extinction trials would be required to meet the criterion for extinction over the same intervals of time. Such relearning and extinction curves ought to have the same general characteristics if they are both measures of the same thing: retention of, or habit strength of, the originally learned problem. A comparison of Figures 1 and 2 indicates a decline in retention in the first half of each curve, but in comparing the second halves, the relearning curve has leveled out, and the extinction curve continues its steady decline. Exactly the same sort of relationship is shown between the two curves whether we compare groups which had interpolated training or groups which did not have such training. The only notable difference is that rats which underwent interpolated training were slower to extinguish the original problem than were rats which did not have such training.

Groups which underwent extinction relearned the problem in approximately the same time as groups which did not undergo extinction. If any transfer of learning occurred, from extinction to relearning, evidently the positive and negative effects were of such strength as to cancel each other, with the result that the total results showed no effect at all. If one considers extinction to be a method of producing loss of retention or habit strength, then our animals which underwent active extinction should have showed a loss of retention greater than that produced by a control group in the same interval of time; there should have been some addition of the loss correlated with the interval of time and the loss produced by extinction. But such an additive process did not take place.

If one considers extinction to be a new form of learning—learning to make other responses in a given situation without a necessary loss of retention of the original learning—the equal relearning scores of our extinction and control groups would tend to support the hypothesis of Finch and Culler (1) that in extinction the pattern of learned responses is still intact but is not being adequately "energized."

If one considers extinction to occur as a result of competition between response systems (2, 6), one would expect this competition of responses to carry over to the relearning procedure, effecting a decrement in relearning scores as compared with the relearning scores of a control group. In our experiment such a decrement has not occurred.

If one considers extinction to be a process of building up reactive inhibition and units of conditioned inhibition (4, 3), one would expect an additive result between the extinction process and the interval of time, producing a decrement in relearning scores as compared with relearning scores of a control group. Such a decrement does not occur in our experiment.

We have noted before that our maze-trained rats required consistently longer to meet the extinction criterion than did control groups. In addition to this phenomenon, which was unexpected, we note that the maze-trained rats pressed the bar more often during extinction than did control rats, although here the trend is not consistent. The maze-trained rats also produced more "aggressive" bar pressings than did control rats. Although the differences of scores only approach statistical significance, the trend is rather strong and consistent and is indicated by a variety of measures. If resistance to extinction is a measure of "habit strength," why do animals which have been trained on a habit which is incompatible with the original habit show greater resistance to extinction of the original habit than do control animals? Learning of the maze habit involved turning away from the lever at the sound of the buzzer, in fact, facing exactly the opposite direction. It involved scratching, pawing, and jumping at the gateway to the maze, and all the responses to be made in the maze itself.

This phenomenon cannot be readily explained on the basis of a habit-family-hierarchy concept, according to which all members of a family of habits tend to be evoked if one member of the family is reinforced in a new situation, because this concept is based upon a fundamental precept that the habits are integrated into a family by means of common fractional anticipatory goal responses. In our experiment there were few if any common fractional anticipatory goal responses uniting the two habits; in fact, they are utterly contradictory. The commonality of the processes resided in the stimulus complex (associated with a hunger drive)—there was no commonality of responses.

It has frequently been suggested that transfer of training from one learning situation to another may be a twofold process, one part of which occurs in connection with learning specific responses, the other part being a process of "adaptation" to the situation, development of techniques, etc.—in other words, there is a transfer of both specific and general factors from one learning situation to another. Such a hypothesis may be applicable to the phenomena under discussion here. General factors in the learning situation (e.g., stimulus complex) may promote positive transfer, at least to a greater extent than the reversal of the specific responses promotes negative transfer. This would account for the fact that our animals which had interpolated training required longer to extinguish than did control animals.

Among the extinction groups, it may be assumed from the evidence in Table 2 that not only was resistance to extinction a function of habit strength in relation to the time-interval variable, but also that the extinction process itself furnished a secondary drive as evidenced by frustration-aggression reactions, and that the strength or persistence of such reactions was directly related to the time-interval variable—the shorter the time between learning and extinction, the greater the frustration. The major difference between the interpolated task groups and control groups during extinction is probably attributable to the fact that the former had had more reinforcements in the general situation as a result of maze training, and with this additional training, their frustration was greater, as shown by the aggressive bar pressings listed in Table 2. A greater number of reinforcements, along with more time spent in the general situation, led for the maze-groups to a build-up of the drive to persist in food-seeking behavior. Thus resistance to extinction may be as much a measure of acquired drives as it is of habit strength.

CONCLUSIONS

The present experiment was designed to investigate the role of experimental extinction as a measure of retention or habit strength. The procedure was designed to compare experimental-extinction measures with relearning scores after certain intervals of time, under normal conditions and under conditions designed to produce retroactive inhibition.

The *S*s of the experiment were 244 rats, divided into 12 groups of approximatelv 20 each; these groups were equated at the end of the learning of the first problem, a Skinner-box type problem, on the basis of the number of trials required to reach the criterion, plus other variables.

One-half of these rats learned a subsequent problem, a simple T maze. The entrance to the T maze was from the Skinner box, and the signal for entry was a buzzer, which had formerly served as a cue that the lever was entering the Skinner box.

One-half the rats trained on both problems and one-half the rats trained only on the first problem subsequently underwent extinction of the first problem at various specified intervals of time. Relearning of the original problem took place at predetermined intervals of time.

The results indicated that the extinction process had no measurable effect on the relearning scores, and that learning of the interpolated problem tended to promote increased resistance to extinction of the original problem. Learning of the interpolated problem tended to facilitate relearning of the original problem one day after completion of the interpolated task, but thereafter neither facilitation nor interference is discernible in relation to relearning after interpolation. The variable of time was correlated with greater changes of relearning scores than were the variables of extinction or interpolation. These results are interpreted in terms of the interaction of positive and negative transfer effects from one problem to another, and in terms of acquired drives.

The experiment lends support to the hypothesis that in extinction the pattern of learned responses is still intact but is not being adequately "energized."

The results of this study seem to cast considerable doubt on the validity of the concept which regards extinction scores as measures of retention or habit strength, as is often assumed in the literature. The extinction scores do not show the same relationship to the time intervals as are shown by the relearning scores (which are also usually regarded as an index of retention or habit strength).

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THE PERFORMANCE OF WHITE RATS AS A FUNCTION OF DOMINANCE AND ACCUMULATING ACTIVITY

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The present experiment was designed to study in the rat the relationship of the social dominant-submissive hierarchy to food-pellet accumulating activity.

In most experiments where animals are permitted to store food pellets, an alley leading from the living cage to the storage bin is used. The present experiment does not employ such an alleyway; rather, the animals were permitted to obtain the food pellets directly from *E*'s hand. Thus, to avoid confusion of terminology, the term "hoarding" is not used, and the storing or collecting of food pellets is referred to as "accumulating activity." Nevertheless, it is felt that accumulating activity may be compared with hoarding activity insofar as the animals are storing food in excess of their immediate needs.

Research on this problem is facilitated by the realistic simplicity of the rat's social life and the absence of complex cultural transmission. When rats are "housed" in pairs, a simple type of interaction results in which a hierarchical system arises. The interaction is not entangled with ambiguous language responses, permitting observational techniques to approximate great accuracy. Thus the effects of this simple interaction may be observed on subsequent behavioral patterns.

Munn (8) has stated that an animal is dominant "when it satisfies its needs before or at the expense of others, or when, in face-to-face situations, it induces submissive behavior in others" (8, p. 468). Bruce (1) studied dominance in water and food situations. The results of his experiment show that: (*a*) dominance occurs only when competition is induced by the experimental situation; (*b*) there is a consistent tendency for rats that are dominant in the water situation to be dominant in the food situation; and (*c*) dominance varies with the strength of the motivating stimulus (deprivation).

The development of a dominant-submissive hierarchy was studied by Seward (10, 11, 12). He states that aggressive and submissive behavior is "*produced by the activation within the organism of two antagonistic disturbances or drives,—here referred to as*—pugnacity *and* fear" (10, p. 191). As a rule, social rank in the dominance hierarchy is established by fighting, bluffing, or passive submission at the initial encounter between the animals, or during an early series of such encounters. Social rank has been attributed to a "marked susceptibility to generalized fear conditioning" (11, p. 222).

The interaction in establishing the hierarchy may influence the subsequent accumulating activity of the dominant and submissive rats. Although hoarding behavior has been explained in terms of the security hypothesis (6) and the deficit hypothesis (7), it becomes necessary to determine, when "security" (situational) and deprivational factors are held constant, what the effects of "inter-rat" relationships will be on accumulating activity.

Morgan, Stellar, and Johnson (7) attempt to minimize the importance of "social factors" in storing food pellets. They state that "deprivation is much more important than any environmental influences or previous experience" for the onset of hoarding in the rat and that "experience plays only a minor role" (7). Experimentation by Miller and Postman (5) failed to show any influence of experience (competition) on the hoarding scores of a group of rats. But recent preliminary experimentation on individual and group hoarding in white rats by Ross, Smith, and Denberg (9) showed that the more submissive members of a group will store less under group conditions than under isolation conditions. Environmental influences of competition seem to lessen their hoarding scores. Dominant members hoarded about the same amount under either condition.

The experiment was directed at the following questions: (*a*) Under conditions involving no food deprivation or food deprivation, will dominant rats accumulate more food pellets than submissive ones? (*b*) Does the proportion of food pellets hoarded depend upon the number of hours of food deprivation?

METHODS

Subjects

Thirty albino rats (Wistar strain) were used in the experiment, 16 females and 14 males, about one hundred days old at the beginning of the experiment. They had been raised in the Connaught Laboratories, University of Toronto. Animal pairs were formed by random matchings. Little variation existed among the pairs because age and weight were nearly the same for all animals. Each pair was housed in a 12-in. by 12-in. metal living cage. The animals were supplied with a plentiful diet of Purina Fox Chow pellets and water. In addition, they were fed small pieces of fresh green vegetables once a week. The pairs remained in their respective living cages for a one-week pretest period. One animal of each pair was marked with carbol-fuchsin stain.

Procedure

Dominance-Submissive Determination

At the end of the pretest period, seven pairs of rats were tested for dominance-submissiveness in a water-deprivation situation, and the other eight pairs, in a food-deprivation situation. After the former were tested in the water situation, they were tested in the food situation, while the latter were tested in the water situation. During a 5-min. testing period, the following measurements were recorded:

Water-deprivation situation. (*a*) The ratio of the number of successful attempts made by a rat to obtain the water tube from its cagemate, to its total number of attempts, i.e., successful plus unsuccessful attempts. (By the use of a wire "baffle" with a small opening to the water tube, only one animal was able to drink at a time.) (*b*) The number of seconds in each 5-min. interval during which an animal maintained control of the water tube.

Food situation. (*a*) The ratio of the number of successful attempts made by one rat to obtain the food pellet from the other, to the total number of attempts, i.e., successful and unsuccessful. (*b*) The number of seconds in each 5-min. interval during which one animal of a pair controlled the food pellet by having it between its teeth or in its paws.

To be selected as dominant one animal had to excel in all four measures mentioned above.

The cagemates were observed in their respective living cages during the contest for a single food pellet or for the water tube, presented at the end of each deprivation period. The food pellet was presented so that when both animals "had their teeth in the pellet" at the same time, the pellet was released.

The animals were tested without food deprivation and then at 7, 14, 21, 28, and 35 hr. of food and water deprivation. The testing schedule was devised so that the rats were mainly tested in the mornings. When the animals were on the hunger routine, they were allowed to eat for 6 hr. before the next food-deprivation period was started. Water was constantly available during the food-deprivation routine. During the water-deprivation routine, the animals were allowed water for 6 hr. before the next water-deprivation period. Dry food pellets were always available during the water-deprivation periods.

Dominance and Accumulating Activity

The cagemates were tested first for accumulating activity at zero hours of food deprivation. An animal was called an "accumulator" if it transported at least one food pellet to the interior of its cage. This definition was arrived at because a pilot study indicated that submissive rats were wont to accumulate very little if at all without food deprivation.

Food pellets were offered by *E* to the animals. This was done by holding one food pellet in either hand at the open door of the living cage and allowing the animals to grasp the pellet. Thus, each paired rat had access to the pellets independently of the other, and there was no physical interference with the accumulating of one animal by the other. The pellets were offered only when both animals were at the front of the open cage. After the first pellets were taken, pellets were offered continually at the front of the cage for 15 min. "Accumulating behavior" was defined as grasping a pellet held at the cage front and transporting it to the interior of the cage.

TABLE 1

Tests of Significance of the Difference between the Mean Number of Pellets Accumulated by the Dominant and Submissive Rats at Various Levels of Food Deprivation ($N_D = 15$; $N_S = 15$)

NO. OF HOURS FOOD DEPRIV.	MEAN NUMBER ACCUMULATED BY D RATS	MEAN NUMBER ACCUMULATED BY S RATS	t	p
0	50.40	3.33	5.38	<.001
7	57.40	3.53	9.16	<.001
14	52.93	2.66	9.66	<.001
21	57.86	3.26	9.16	<.001
28	53.46	1.80	10.94	<.001
35	61.86	1.86	10.37	<.001
42	63.53	2.20	9.89	<.001

The animals were retested for accumulating activity at 7, 14, 21, 28, 35, and 42 hr. of food deprivation, with a 6-hr. satiation period between each interval of deprivation.

RESULTS

Accumulating Activity and Dominance

The data in Table 1 indicate that the mean number of food pellets accumulated by the dominant rats is significantly greater than the mean number accumulated by paired submissive cagemates. The t values indicate that the dominant rat accumulates significantly more food pellets than the submissive one at all levels tested. (This statistic was employed because on using the standard error of the measure of skewness [2], it was observed that the frequency distribution did not depart significantly from the normal curve.) Conditions under which the accumulating tests were carried out insured that all animals had an equal opportunity of obtaining the food pellets.

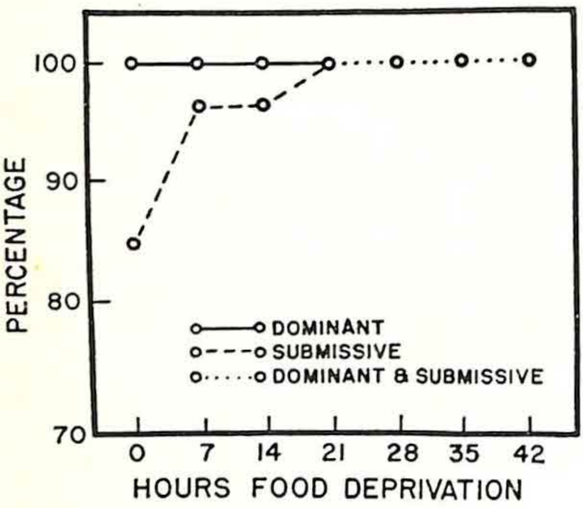

FIG. 1. Percentage of rats accumulating pellets under varying levels of food deprivation

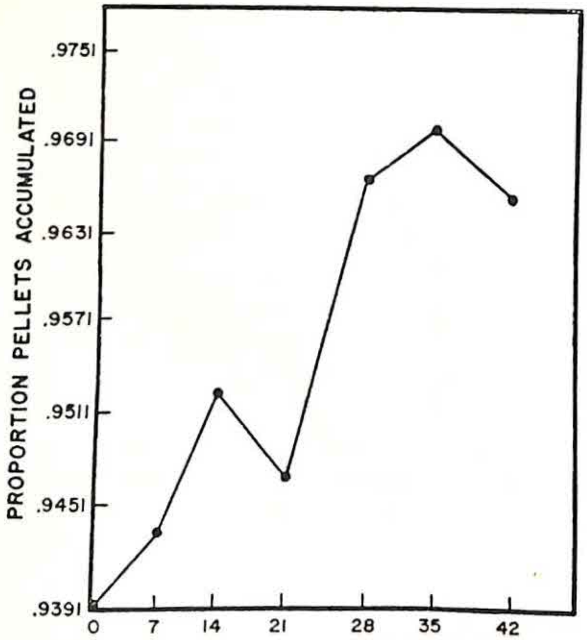

FIG. 2. Proportion of pellets accumulated by dominant rats under varying levels of food deprivation

It was also found that a significantly greater percentage of dominant rats begin to accumulate without food deprivation. The curves in Figure 1 show that the difference in the percentage of dominant and submissive rats accumulating pellets disappears when food deprivation is introduced.

Proportion of Food Pellets Accumulated As a Function of Deprivation

Although there was no significant difference in the proportion of food pellets accumulated by the dominant and submissive rats at successive levels of food deprivation, the curve in Figure 2 suggests a general tendency for the proportion of pellets accumulated by the dominant animals to increase with increased food deprivation. Furthermore, it was found that there is a significant difference ($p = .01$) between the proportion of food pellets accumulated at 28, 35, and 42 hr. of food deprivation, respectively, and the proportion accumulated without deprivation (zero hours).

DISCUSSION

The importance of early adult experiences in the development of the adult accumulating habit may account for the difference in the number of food pellets stored by the dominant and submissive rats.

Two animals randomly paired and placed in a living cage have set up a dominant-submissive hierarchy through a conditioning process (10, 11). Withdrawing behavior and refusal to fight have been conditioned by pain from previous bouts. The reinforcing process of the repeated presence and occasional fights with its cagemate maintained the dominant-submissive hierarchy.

Hoarding, explained by Marx (3, 4) as the acquisition of independent habits through experience, seems to shed some light on the accumulating activity of the dominant and submissive rats. The animal comes from the back of the cage to obtain the pellet; it grasps the pellet with its mouth and carries the pellet to the interior of the cage where it may feed. The pellet seizure is reinforced by a subsequent hunger reduction associated with feeding. Direct sensory and olfactory reinforcements are produced by the pellet-seizure response. Thus to acquire the hoarding habit, or in this case the accumulating habit, the animal must experience these events.

In this social situation which has been set up between rat pairs, competition for the pellet of food exists. Since dominant-submissive behavior was determined by having rat pairs fight for a single food pellet, then the presentation of food pellets to be stored may be expected to rearouse the emotional reactions associated with the initial food-pellet presentation. Associated with the initial pellet presentation is the vigorous and usually successful attempt made by the dominant rat to grasp the pellet from the jaws of the submissive rat.

The progressive accumulation of inhibitory factors associated with (*a*) the social situation, i.e., pain from fights with the ever-present dominant cagemate, and with (*b*) the presentation of food pellets to be accumulated, i.e., the submissive rat is conditioned to kinesthetic stimulation produced by the pellet seizure by the dominant rat, and (*c*) a failure at times, to leave the back of the cage, prevented the submissive rat from strengthening or at times acquiring the necessary experience leading to successful accumulating. A fear response was observed as part of submissive rats' behavior toward the pellets, i.e., a "jerky" forward and backward movement toward the offered pellets, or a cowering in the rear of the cage.

The dominant rat carried the food pellets to the interior of the cage; it nibbled on the first few pellets it accumulated, but returned to obtain more pellets. While accumulating pellets from the front of the cage, the dominant rat would also usually grasp the food pellet from the submissive rat and put it in its own "pile." The successive reinforcements of the pellet-seizure response, of the minimization of frightening stimuli associated with the presentation of the food pellets, and of the social situation, served to strengthen the accumulating habits in the dominant rats.

SUMMARY AND CONCLUSIONS

The experiment was designed to determine the effects of the dominant-submissive hierarchy on the accumulating activity of a group of randomly paired rats. The experiment led to the following conclusions:

1. The dominant rats accumulate more food pellets than the submissive ones at all levels of food deprivation tested, namely 0, 7, 14, 21, 28, 35, and 42 hr.
2. There were no significant differences between successive levels tested in the proportion of food pellets accumulated by the rats.
3. There was a significant change between the proportion of food pellets accumulated without food deprivation (zero hours) on the one hand, and the proportion accumulated at 28, 35, and 42 hr. of food deprivation, respectively, on the other.
4. A larger percentage of dominant rats than submissive ones accumulate food pellets without food deprivation.

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EFFECTS OF EARLY EXPERIENCE ON MATING BEHAVIOR IN MALE RATS[1]

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It has been established that male rats reared in isolation from weaning to sexual maturity are capable of normal copulatory behavior when placed with a receptive female (2). Although practice or learning is not necessary for biologically adequate coital responses there is evidence indicating that the sexual behavior of adult males of this species may be altered by the conditions under which the animals are reared. Rats that mature in individual cages are more likely to copulate than rats raised in the same cage with females or males (2). In an unpublished experiment F. A. Beach and P. Rasquin reared males in isolation from weaning to adulthood but exposed each animal to another rat of the same age for 10 min. a day at regular intervals. They found that males subjected to such treatment were much less likely to copulate in adulthood than control animals raised alone or in group cages. Experiments reported in the present paper represent attempts to verify earlier findings and to examine systematically the factors involved in the inhibition of normal sexuality as a result of certain types of prepuberal experience.

EXPERIMENT I

Method

Forty-six male rats of the Sprague-Dawley strain were kept in individual cages from 30 to 160 days of age. Once each week every male was placed in a circular observation arena and allowed 10 min. for exploration of the testing environment. At the conclusion of this adaptation period a female rat the same age as the male was placed in the arena. Stimulus females were rendered sexually receptive by injections of estrogen and progesterone.[2] The test was terminated after 10 min. unless the male had shown complete or incomplete copulatory responses, in which instance observations continued for 10 min. from the initiation of coital activity.

Results

At the conclusion of the tenth test the males were 100 days old, at least one month older than the age at which adult copulatory behavior usually appears. But at this stage in the experiment only 5 (10.9 per cent) of the group had shown any mounting activity, 4 (8.7 per cent) had achieved intromission, and only 2 (4.3 per cent) had ejaculated. At 160 days 12 (26.1 per cent) had shown mounting activity, 9 (19.6 per cent) had achieved intromission, and 3 (6.5 per cent) had ejaculated. It was noted that the adult males frequently responded to receptive females with the wrestling, chasing, and mock-fighting behavior typical of prepuberal rats.

Because the sexual activity of the experimental males was so restricted, it seemed advisable to determine the frequency of copulatory reactions in stock males of the strain employed. We administered five sex tests to 15, 100-day old Sprague-Dawley males that had been reared in sex-segregated groups from 21 days of age. Of this number 46.7 per cent achieved intromission, and 33.3 per cent ejaculated. This is an appreciably higher score than that recorded for the experimental population, although it represents a much lower degree of sexual activity than can be found in some other strains.

There was no reason to suspect that the subjects in Experiment I were physiologically abnormal. However, with some male rats that fail to copulate the behavioral defect can be remedied by supplying the animal with large amounts of exogenous hormone (1). For this reason some of the noncopulating rats in the present experiment were injected with testosterone propionate and tested again for sexual activity. The sexual behavior of castrated male rats is restored to preoperative levels by daily injections of 75 micrograms of this material (3).

Seven of the noncopulating males in Experiment I received five daily injections of 500 micrograms and were tested with receptive females 24 hr. after the final injection. Five of these rats showed no sexual behavior after androgen treatment, 2 mounted the female, and 1 achieved intromission. There were no ejacula-

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[1] This investigation was supported by a grant from the Rockefeller Foundation.

[2] The hormone preparations used in this study were generously supplied by Dr. Edward Henderson of Schering Corporation, Bloomfield, N.J.

tions. Ten additional males that had never mounted the female were given daily injections of 500 micrograms for 10 days. Twenty-four hours after the last injection 1 male copulated and ejaculated, but the remaining 9 were sexually inactive. Ten control noncopulators given injections of inert sesame oil showed no behavioral change.

The extremely limited behavioral response to such large amounts of androgen indicates that the initial failure to copulate cannot be referred to an androgen deficiency. It appears more probable that the infrequency of coital reactions was due to some inhibiting influence exerted by our methods of rearing and testing the experimental males. To analyze the possible sources of such inhibition, the second experiment was conducted.

EXPERIMENT II

Method

Fifty-seven male albino rats of the Sprague-Dawley strain were maintained in individual cages from 36 days of age until completion of the experiment. The animals were divided into four groups, and beginning at 37 days of age and continuing for 9 weeks, the members of three groups were subjected to weekly "conditioning tests," as indicated in Table 1.

Conditioning tests for males in Group A were conducted in the same fashion as the mating tests described for Experiment I. Group B males were left in the testing arena with their masculine partners, and any homosexual behavior that occurred was recorded. Rats in Group C simply spent 10 min. each week alone in the arena.

Beginning one week after the ninth conditioning test all members of each group were subjected to a series of weekly "critical tests." During the critical tests each male was observed with a female of proven receptivity, and the procedure followed was that described for Experiment I.

As soon as a male demonstrated its sexual capacity by ejaculating within the time limits of the observational period, it was not tested any further. Those animals that made no sexual responses (i.e., mounting the female) in five successive critical tests were also discarded. Males that had copulated or attempted to do so but had not ejaculated in the course of the first five critical tests were given four weekly exposures to receptive females from the week in which their first coital response occurred. This plan resulted in the conduction of seven critical tests, but by the time of the sixth and seventh test all but nine males had been eliminated, because they had ejaculated or had failed to display any mating responses whatsoever.

Results

During the conditioning tests one male in Group A copulated with the receptive female and three additional males displayed incomplete coital attempts. There were no ejaculations. All four of these males copulated in the critical test series. One animal in Group B mounted its masculine partner during the conditioning tests, and this rat failed to copulate with the female in the critical tests.

Proportion of each group copulating and ejaculating. Figure 1 shows that there was no marked difference in the number of males in various groups that displayed the copulatory response at least once during the critical tests. But Groups A and B, both of which had been exposed to other rats during conditioning tests, contained fewer ejaculators than the other two groups. The figure reveals a clear-cut trend of increasing percentage of ejaculators as Groups A, B, C, and D are considered sequentially. The proportion of each group showing incomplete copulatory reactions ranged from 46.7 per cent in Group B to 53.8 per cent in Group A, but

TABLE 1

Weekly Conditioning Tests

GROUP	*N*	PROCEDURE IN CONDITIONING TESTS
A	13	Tested with receptive female of own age
B	15	Tested with a male of same age and weight
C	14	Placed alone in the testing arena
D	15	No tests or exposure to testing arena

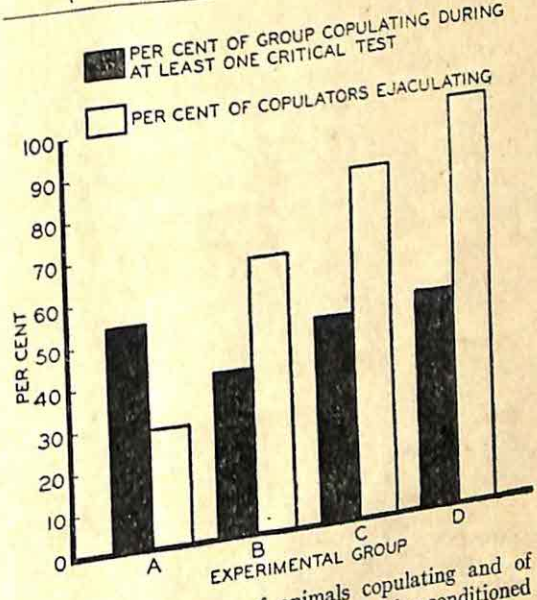

FIG. 1. Percentage of animals copulating and of copulators ejaculating in Group A, males conditioned with females; Group B, males conditioned with males; Group C, males in arena alone; and Group D, males isolated.

there was no trend or consistency in the comparisons.

To assess the statistical significance of intergroup differences in the number of ejaculators, the chi-square test, corrected for continuity, was applied. The values involved were the number of animals in each group that ejaculated at some point in the critical tests. Two differences were found significant at the .05 probability level. Group A differed significantly from Group D; and when the combined frequencies from Groups A and B were contrasted with the combined scores of Groups C and D, the difference was also reliable. This method of combining scores seems permissible because Groups A and B had in common the factor of previous exposure to a stimulus animal whereas members of the other groups lacked this experience.

TABLE 2

Relative Copulatory Performance of Different Groups during the Critical Tests

GROUP	NUMBER OF COPULATORS	AVERAGE NO. OF CRITICAL TESTS PRECEDING THE FIRST TEST IN WHICH COPULATION OCCURRED*	NO. OF MALES FAILING TO COPULATE IN ONE OR MORE TESTS AFTER THE FIRST OCCURRENCE OF COITAL ACTIVITY**	AVERAGE FREQUENCY OF COPULATORY RESPONSES IN TESTS IN WHICH SUCH BEHAVIOR OCCURRED**
A	7	1.14	5	5.78
B	6	1.17	4	6.51
C	7	0.43	1	7.96
D	8	0.75	1	10.06

* Difference between scores of A + B and C + D not statistically significant.

** Difference between scores of A + B and C + D significant at .01 level.

TABLE 3

Performance of Different Groups during the Test in which Ejaculation Occurred

GROUP	NO. OF EJACULATORS	AVERAGE NO. OF TESTS FROM FIRST COPULATION TEST TO TEST IN WHICH EJACULATION FIRST OCCURRED	AVERAGE NO. OF TOTAL COITAL RESPONSES	AVERAGE FREQUENCY OF COITAL RESPONSES PER MINUTE
A	2	3.50	15.00	1.69
B	4	2.75	15.25	1.85
C	6	2.67	18.00	3.17
D	8	1.63	17.37	2.16

Differences in copulatory behavior. Although there were no significant intergroup differences with respect to the number of animals showing some copulatory behavior, there were distinct variations in the timing and frequency of coital responses. Rats in Groups C and D initiated copulatory reactions fairly early in the critical test series. When a male in either of these groups had copulated without ejaculation in one critical test, it was likely to copulate in subsequent exposures to the receptive female. Neither of these statements applies to animals in Groups A and B. During tests in which coitus took place the frequency of copulations was higher for Groups C and D than for males in the other groups. These differences are summarized in Table 2.

Differences in ejaculation behavior. As noted earlier, the experimental groups differed with respect to the proportion of males achieving ejaculation. When attention is confined entirely to those males proved capable of ejaculating, intergroup differences still exist. Ejaculators in Groups C and D reached the point of sexual climax sooner after that critical test in which they began to copulate than did the animals in Groups A and B. During tests in which ejaculation occurred the average total number of sexual responses was higher for Groups C and D than for A and B. Furthermore, the average frequency of mating reactions per minute of observation was higher for C and D than for the other groups. These intergroup differences are summarized in Table 3.

The number of ejaculators was small, and this may partly account for the fact that none of the differences shown in Table 3 meets the test of statistical significance. Nevertheless, the trends in each instance are consistent and show that males in Groups A and B were sexually less active than members of the other two groups even when only the ejaculating animals are considered.

Effects of androgen treatment. Twenty males that failed to ejaculate were given seven daily injections containing 1,000 micrograms of testosterone propionate and tested with receptive females 24 hr. after the final injection. Androgen was administered to 8 males that had copulated but had not ejaculated and to 1 that had shown only incomplete copulatory responses. Three rats in this group achieved an ejaculation in the postinjection test. Of 11 males that had never attempted copulation, 4 ejaculated after androgen administration. There was no indication that differential treatment during the conditioning period had any influence upon responsiveness to the hormone injections.

DISCUSSION

The performance of males in Experiment I and Group A in Experiment II suggests that certain behavioral tendencies or habits established before puberty are capable of interfering with execution of the complete masculine sexual response in adulthood. Under the conditions imposed in these experiments periodic exposure of immature male rats to estrous females of their own age greatly reduced the probability that such males, at maturity, would display the ejaculatory reflex when tested with receptive females. The tendency to copulate and to effect intromission was not lost, but the frequency of coital contacts in a time-limited test was definitely reduced. It appeared that this was due in large measure to the persistence of competing play responses characteristic of the immature male. Adult animals frequently reacted to the receptive female by wrestling, pawing, and climbing over her, and in general displaying the playful responses which typify social interaction between prepubescent animals.

The inhibiting effect of these competing behavior tendencies was evident even during those tests in which copulatory responses occurred. The normal male rat usually mounts and penetrates the estrous female several times in rapid succession. Behavior intervening between copulations consists chiefly of autogenital cleaning and pursuit of the female. Ejaculation usually occurs at the conclusion of a series of closely spaced copulatory contacts. The copulatory responses of the experimental animals to which we have been referring were widely spaced in time. After one or two intromissions most males shifted to the play pattern and resumed copulating only after considerable delay. Consequently, there was less than the usual opportunity for a cumulative increase in sexual excitement which normally culminates in ejaculation.

Results obtained with males of Group B in Experiment II show that adult sexual activity can be depressed by the appropriate sort of prepuberal exposure to masculine as well as to feminine partners. In this instance again a specific set of response tendencies appears to become strongly associated with the testing experience—that is, with brief, weekly periods of contact with another rat in a constant and unique environmental setting. At the time that these habits are formed the prepotent acts in the immature animal's behavioral repertoire are the playful responses mentioned above. When males in Group B reached adulthood, they were confronted with receptive females under the same conditions and in the same setting that previously had been associated with playful interaction with a masculine stimulus animal. Competing tendencies toward play and copulation were aroused. The results were qualitatively comparable to those described for rats in Group A, but there were several quantitative differences between the two groups.

In Group B, as contrasted with Group A, a higher percentage of copulating males eventually achieved an ejaculation (Fig. 1). During tests in which copulation occurred, the average number of such responses was slightly higher in Group B than in Group A (Table 2). Of those males that eventually effected ejaculation, Group B animals did so earlier in the critical test series, and in the test with ejaculation Group B males showed a slightly larger number of coital responses and a greater frequency per minute (Table 3). Most of these differences are small, and none approaches statistical significance. They deserve mention because they indicate the possibility that the prepuberal conditioning of Group A may have exerted a more powerful inhibiting effect upon sexual performance in adulthood than did the somewhat different treatment of Group B. A difference in the direction indicated might be expected inasmuch as the stimulus situation in critical tests for Group A was identical with that prevailing during prepuberal conditioning, whereas Group B animals were conditioned to other males and received estrous females in the critical tests.

There was little reason to anticipate that the behavior of rats in Groups C and D would differ significantly in the critical tests. There was the remote possibility that Group D males would be temporarily distracted by the novelty of the testing arena and might therefore fail to respond promptly to the receptive female. The data show that Group D animals began mounting behavior about 2 min. after being placed with the receptive female, while Groups A, B, and C each had an initial latency of approximately 1 min. This suggests that the novelty of the situation did have an inhibiting effect on the completely isolated animals. However, the percentage of copulators achieving ejaculation was higher in Group D than in Group C (Fig. 1). During tests in which copulation occurred the average frequency was higher for Group D (Table 2). Group D rats tended to reach the point of ejaculation somewhat earlier in the critical test series than did members of Group C (Table 3). Various limitations of the data render any interpretations of these small differences so speculative as to be worthless. The most significant and important comparisons in Experiment II are those between Groups A and D and between the combined averages of A and B compared with C and D.

SUMMARY

In two experiments a total of 103 male rats were reared in individual cages from infancy to adulthood and at weekly intervals 57 of these animals were placed for 10 min. with a sexually receptive female of their own age. Fifteen rats were exposed to other males instead of females in the weekly tests and members of two control groups were not exposed to any other rats until adulthood was reached.

Beginning when they were 99 days old all males were observed in a series of mating tests with receptive females. There was no significant difference between groups as far as the occurrence of copulation was concerned, but the ejaculatory reaction was infrequent in males that had been periodically exposed to either females or males during the prepuberal phase of life.

The sexual inferiority of rats in the experimental groups was due in all probability to conflicting behavior tendencies resulting from habits formed during the prepuberal tests. The evidence points to the conclusion that in tests conducted before puberty the experimental males formed habits of playful wrestling, pawing, and climbing over a second animal. These weekly 10-min. tests constituted the only opportunity for formation of response tendencies toward a second rat. As a result, the habit of reacting playfully toward another animal was so strongly ingrained that it persisted in adulthood and interfered with a competing tendency to copulate when the partner was a receptive female.

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EFFECTS OF PREVENTING INTROMISSION UPON SEXUAL BEHAVIOR OF RATS[1]

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Many experiments have shown that the sexual behavior of lower mammals depends heavily upon hormones from the reproductive glands (5). In fact, an appropriate endocrine balance is a *sine qua non* of copulatory behavior in many species. Studies of the sensory basis of such behavior in rats suggest that distance receptors are involved but that direct bodily contact is of prime importance in the final phases of the coital relationship (4). This study deals with one type of stimulation, namely, that derived from penetration of the vagina by the penis.

It is usually assumed that the execution of normal mating responses by male and female animals depends in part upon direct stimulation of the genitalia. The literature contains several reports which, taken together, suggest that males and females may differ with respect to the importance of genital sensations, and that different portions of the masculine coital pattern depend upon different sorts of stimulation. Ball (1) noted normal sexual behavior in four of five female rats from which the ovaries, uterus, and vagina had been removed. No quantitative records were reported, but all of the elements in the normal female's sexual repertoire were observed in these animals after injections of estrin. Koster (7) treated immature female rats with androgen, thus preventing the formation of a normal vagina. When such animals were tested in adulthood with sexually vigorous males, copulatory responses sometimes occurred, and in one instance a single male displayed the ejaculatory reflex while copulating with a modified female. Beach (3) described the sexual behavior of one female rat with congenital absence of ovaries, uterus, and vagina. When injected with ovarian hormones and placed with a male, this animal executed all the behavioral responses normally associated with estrous. Although none of the reports mentioned here included systematic, quantitative measures of behavior, all of them point to the conclusion that sensations deriving from penetration of the vagina are not essential to the female rat's continued sexual responsiveness.

Male rats that are prevented from achieving intromission may continue to attempt copulation with a receptive female. Beach and Holz (6) castrated males of this species on the day of birth, injected them with androgen during adulthood, and tested their responses to receptive females. Under the influence of the exogenous hormone, experimental males executed many copulatory attempts but, with one exception, never displayed the ejaculatory response. Ejaculatory failure was presumed due to underdevelopment of the penis which, despite hormone treatment, remained of infantile size. It was assumed that intromission occurred rarely if at all, and that the resulting lack of genital stimulation prevented the achievement of sexual climax. To check this interpretation, these investigators tested several adult, noncastrated males for sexual behavior and then subjected them to an operation in which a section of the *os penis* was removed. In postoperative tests the males continued to mount and attempt to copulate with receptive females, but ejaculatory responses were not present.

In the present investigation quantitative comparisons were made between the behavior of rats with normal vaginas and experimental females lacking all accessory sexual structures including the vagina. In addition, the responses of normal males to these two types of stimulus animals were studied.

METHOD

Twenty-one females were ovariectomized. In 10 of these animals the tubes, uterus, and vagina were also removed, and the edges of the external wound were clamped together until it had healed and no opening

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[2] The author wishes to express deepest appreciation to Dr. Frank A. Beach for his many helpful suggestions in the design of this study and his invaluable help in the writing of this paper.

remained. When recovery was complete, control and experimental females were brought into heat by the injection of .033 mg. of estradiol benzoate followed 72 hours later by .50 mg. of progesterone.[3] Eight hours after the second injection, tests for sexual behavior were initiated. Before formal observations were begun, a series of selection tests was conducted to make certain that all males were potent and all females were responsive to the hormone treatment to the extent of displaying prompt signs of receptivity. For females the criterion was the assumption of the lordosis position during at least two of the male's first six mounting responses. Males were required to ejaculate when tested with a normal, receptive feminine partner. After the first test in which it ejaculated, a male was entered in the experiment proper. Animals that did not ejaculate by the fourth preliminary test were eliminated.

Experimental and control females were tested with males once a week. Males were tested at three- or four-day intervals, being exposed to an experimental female on the first formal test and to a control female on the second. If a male ejaculated on the second test, it was subsequently paired with experimental and control partners alternately in subsequent tests. Males that failed to ejaculate with the control female on the second test were given a control animal on the third test, and continued to be paired with control females until ejaculation did occur or until four tests without ejaculation had been recorded. In the latter instance the male was discarded. All the females were tested at least four times. Every male was tested with at least three experimental and three control females, and five of the males were tested as many as five times with each type of stimulus animal.

Mating tests were always conducted during the dark phase of the rats' 24-hr. light-dark cycle. They took place in a circular arena 30 in. in diameter. If no copulatory attempts occurred during 10 min. after the male and female were put in the arena, the test was terminated and scored as negative. If copulation was attempted, the test lasted until ejaculation, or, if the male did not ejaculate, for 15 min. from the time of the first copulatory attempt.

Behavioral items scored for the females were as follows: assumption of lordosis, hopping, ear-wiggling, running away from the male and then stopping until he approached, approaching the male and nosing his body or assuming a position directly in front of him, turning toward the male while being pursued by him. The four types of response recorded for the males were incomplete copulations in which intromission did not occur, copulation with intromission, copulation with ejaculation, and discrete periods in which the male licked the female's genital region.

RESULTS

The readiness with which a female displays lordosis is revealed in the Copulatory Quotient, which is calculated by dividing the number of lordosis responses by the number of times the female was mounted by the male, and multiplying by 100 (2). For control females the mean CQ in all tests which included mounting by the male was 98.8. The same measure for experimental females was 102.1. The average frequency of approach responses per minute of observation was 0.58 for control and 0.50 for experimental females. Ear-wiggling reactions occurred on the average 1.75 times per minute of observation in the case of control animals and 1.73 times in the records of experimental females. Hopping, running, and turning scores for the control and experimental females were also very similar. To evaluate the significance of the small differences between the two groups, the *t* test for differences between independent means was employed using two tails of the normal distribution. None of the differences, nor the direction of the differences, proved to be statistically significant. When all the "provocative responses" (i.e., all receptive reactions with the exception of lordosis) were combined, the differences between control and experimental groups were found not to be significant.

In comparing the reactions of males to experimental and control females, it was necessary to combine scores for incomplete and complete copulations, for insertion was impossible when a male was paired with an experimental female. Ejaculation occurred in 50 to 100 per cent of the tests with control females and never took place when the stimulus animal was an experimental female. Despite the absence of ejaculation, males continued to attempt copulation with the experimental females. The average number per minute of copulations plus attempted copulations was 1.81 with control partners and 1.90 with experimental females. The difference was not statistically significant.

Demonstration of the fact that female and male rats execute copulatory responses under conditions in which intromission is impossible emphasizes the probable importance of nongenital stimulation for the arousal and maintenance of sexual excitement. It seems likely that provocative activities of the estrous female and the attentive responses of the male provide the basis for continued sexual interaction in the absence of intromission. The behavior of a pair reveals a reciprocal relationship in which some act by one partner evokes a complementary response on the part of the other, and maintenance of a high level of excitement depends upon mutual interaction involving various forms of stimulation.

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[3] The hormone preparations were generously supplied by Dr. Edward Henderson, Schering Corporation.

To measure this type of relationship, the number of provocative responses by the female and the attentive responses by the male (mounting the female or licking her genitalia) were compared in two ways. First, the male's behavior was considered the independent variable and the female's reactions the dependent one. The number of provocative responses shown by different females toward the same male were correlated with that male's attentive reactions. Such correlations should reveal any effect of a given male's behavior upon the behavior of different feminine partners. If the Pearsonian coefficients were randomly distributed, their mean would be zero. Therefore, a *t* test was applied to the mean correlation of all of the males, using individual correlation coefficients as scores. The scores of all females, control and experimental, were combined, and the mean correlation obtained in this manner proved to be significant at the 4 per cent level of confidence. This suggests that an attentive male is likely to evoke more provocative responses from an estrous female than is a less attentive partner.

Next, the female's behavior (i.e., total provocative responses) was taken as the independent variable, and the attentive reactions of different males to each female were used as the dependent variable. The mean correlation obtained was significant at the 1 per cent level of confidence, indicating that females with high provocative scores tend to elicit more attentive reactions than do those that make fewer advances to their masculine partners.

SUMMARY

Ten female rats were subjected to an operation in which the ovaries, uterus, and vagina were removed. In a control group of 11 females the ovaries were removed, and members of both groups were brought into heat by hormone injections. The sexual behavior of these animals was measured in a series of mating tests with normal males. The amount and kinds of sexual activity did not differ for the two groups, indicating that sensations derived from vaginal stimulation are not essential to the display of receptive behavior. Males attempted to mate with females from both groups with equal frequency. However, when tested with females lacking a vagina, males did not display the ejaculatory reflex. It is apparent that genital sensations are not necessary for heat behavior in the female and that absence of stimulation derived from insertion does not deter the male from attempting to copulate. However, stimulation of the penis by the vagina is exceedingly important if the final response of ejaculation is to occur.

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THE EFFECTS OF AUDITORY STIMULATION UPON THE IMMEDIATE RETENTION OF A PREVIOUSLY LEARNED MAZE BEHAVIOR IN THE ALBINO RAT

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Exposure to auditory stimulation that is intense enough to produce some instances of seizure in the white rat appears to affect the reperformance of a previously learned maze pattern. Of interest in this problem is the question whether such stimulation (*a*) affects retention of the learned pattern, or (*b*) produces other effects, e.g., convulsions, which in turn affect retention.

Griffiths (2) investigated this problem using both a closed and an open maze and concluded that with the exception of the closed maze "... auditory stimulation, of convulsive or nonconvulsive rats, instead of inhibiting repetition of the maze habit, has actually facilitated it" (2, p. 281). Griffiths also observed that his convulsive rats, when run on the closed maze, exhibited a certain amount of immobility, passivity, and shelter seeking. This behavior increased the running time of these rats on the criterion trials.

Maier and Wapner (3) also exposed a group of rats to a loud noise after they had learned to run a closed maze. As in the Griffiths experiment, the rats which had convulsions took significantly longer to run the criterion trials. In addition they made more errors.

A tentative conclusion to be drawn from these experiments is that retention of the pattern of a closed maze is affected by convulsions produced by auditory stimulation. However, such a conclusion is inconsistent with what the convulsive rats did on the open maze. In order to clarify the matter, let us assume that the convulsive rats ran the open maze faster in order to gain the shelter of the closed food box. Such an assumption allows us to suggest that the performance of the convulsive rats on the closed maze was brought about by the presence of an intervening variable, namely fear, and that retention of the learned pattern was not measured by that performance.

The purpose of the present experiment is to test this assumption by introducing certain modifications into the open maze which would allow the convulsive rats to exhibit the fear response clearly, and at the same time would make it possible to test for retention of a previously learned habit.

METHOD

Apparatus

The apparatus used for this experiment was a modification of the Tolman, Ritchie, and Kalish (6) place-response maze. Since the *E*s desired to work with a maze which involved a simple discrimination problem, the essential features of the maze were left intact. However, certain changes were made. "Shelter" tunnels were added and the food boxes left uncovered (see Fig. 1). The rationale behind these changes was based upon the following presumption: If, when motivated by hunger, auditory stimulation facilitates the performance on the maze, both the convulsive and the nonconvulsive animals should readily go through the tunnel to the food box. On the other hand, positioning the tunnels beyond the choice point allows for an unequivocal test of retention for the convulsive rats and at the same time makes it possible to demonstrate the presence of fear.

Subjects

The *S*s were selected from a colony of about 125 rats. Sixteen rats were placed in the control group. The experimental groups of convulsive and nonconvulsive rats were built up to 9 and 12, respectively. It is sometimes difficult to get enough convulsive rats. Sisk (4) found only 3 out of 17; Maier and Wapner (3) found 10 out of 26; and Stainbrook and Loewenbach (5) found 3 out of 18. In the present study 5 out of the first 10 rats receiving auditory stimulation had convulsions. The remaining 4 convulsive rats were obtained only after training 14 additional rats.

All these rats were albino males averaging approximately 100 gm. in weight at the start of the experiment.

Procedure

In the beginning the rats were fed daily in their home cages until it was relatively certain that adaptation to the environment had occurred. During this period, approximately two weeks, the rats were handled frequently. Following this, the animals were introduced to the maze by placing them on the open feeding stand and allowing them to discover food. They were then removed from the stand and placed just before the entrance to the "shelter" tunnel. From there the rats had to go through the tunnel and pass the black curtain to get to the feeding stand. This procedure was repeated on the opposite feeding platform of the maze. After this introductory period, the animals were deprived of food every other 24 hr. Experimental days were held every other day with the exception of Sundays and holidays.

During the experiment, feeding platform F_2 (see Fig. 1) was blocked by B. The rats were confronted with a place-learning task, i.e., when the rat was placed at starting point (S_1), it had to make a right turn at the center point (C) to make the correct response to get food on platform (F_1). When placed at S_2, the animal had to make a left turn at C to get to F_1. Food was kept on both feeding platforms throughout the entire experiment.

The animals were given 6 trials every experimental day until the criterion of 9 out of 10 consecutive errorless trials was reached. Each successful endeavor to get to F_1 constituted a trial. After the end of each trial, the animal was brought back to the starting point until six such trials were made for that day. Series of starting points consisted of the pattern S_1, S_2, S_2, S_1, S_1, S_2, and S_2, S_1, S_1, S_2, S_2, S_1. Where the former series was given one day, the latter series was given on the next experimental day. After each entrance upon F_1, the animals were allowed to eat food for 15 sec. While the animals were on the feeding stand, they were fed small pellets of dog biscuits saturated with milk. At the end of the sixth trial, the animals were returned to their home cages, where they were given the remainder of their rations, which consisted of dry dog biscuits and water.

Up to this point both experimental and control groups were identically treated. When the criterion of 9 out of 10 consecutive errorless trials was met, each experimental animal was taken individually to another room where it was subjected to 5 min. of auditory stimulation consisting of jingling 15 keys over the animal's cage. The S was then given a 20-min. rest period after which it was returned to the experimental room and given 3 additional, or retest, trials. The control group was similarly treated except that it received no auditory stimulation. Each control S was kept in this room for 25 min. Following 25 min. of rest, it was returned to the maze for an additional 3 trials.

During the three retest trials, the animals were permitted to eat food for 15 sec. when upon the feeding stand. Before each retest trial, they were given a 2-min. rest period. Time and error scores were recorded for all trials.

Method of recording time and error scores. Time was taken from the moment the animal was placed upon the starting point until it reached the feeding stand and began to eat.

The following were recorded as errors:

1. In the beginning some animals would not leave T_2. In order to expedite the learning process, the animals were forced out by tapping the top of the tunnel with a pencil. When such action was required, it was recorded as an error. This behavior in the rat disappeared as the animal became more familiar with the maze.

2. Any response toward the F_2 side of the maze constituted a second form of error. C was more or less considered as a neutral area.

3. Depending upon which side of the maze was considered the starting point for that trial, any behavior directed to the opposite end constituted a third form of error. Retracing within the confines of the starting alley and the center point of the maze was not classified as an error. Before retracing was classified as an error, the animals had to have four feet in the C area.

4. Climbing on top of the tunnel, whether it was on the F_2 or F_1 side of the maze, comprised the fourth possible error on this maze.

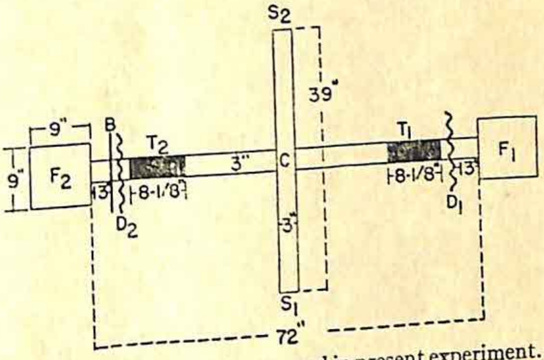

FIG. 1. Diagram of maze used in present experiment. Elevated maze: S_1 & S_2: Starting points; F_1 & F_2: Open feeding platforms; C: Center point; B: Block-off piece, 7-½ in. wide; D_1 & D_2: Black curtains; T_1 & T_2: Shelter tunnels, 3-¼ in. high.

TABLE 1

A Summary of Trials to Reach Criterion and Time and Error Scores on the Three Retest Trials

MEASURE	CONTROL 16	NON-CONVULSIVE 12	CONVULSIVE 9
Mean trials to learn	41.3	36.5	31.4
Mean time to run retest trial (sec.)	36.3	34.2	1641.6
Mean errors retest trials	1.1	1.2	1.0

RESULTS AND DISCUSSION

Quantitative Results

Results are presented in Table 1. The three groups do not differ significantly in the number of trials taken to reach the criterion. The largest difference is between the control group and the convulsive group, but the significance of this difference is between .10 and .20. Any differences in time and error scores on the retest trials cannot be attributed to difference in the ability of the groups to learn the maze.

The average time to run the retest trials shows that the control group and the nonconvulsive group do not differ appreciably. The significance of the difference between the convulsive group and the control group is less than .01. This result confirms the findings of others (5, 4, 3, 1).

The results on the particular maze used in this study support the contention of Maier and Wapner that the increased time taken by the convulsive group is due to the "...superposition of fear on the learned pattern rather than the loss of a learned pattern" (3, p. 34).

This contention is further strengthened by the fact that none of the differences in error scores between the groups is significant. The greater incidence of errors found by Maier and Wapner can be accounted for by the fact that they used a closed maze. Our results lead us to believe that neither exposure to auditory stimulation nor convulsions affects retention. Furthermore, a test of the effect of auditory stimulation upon retention of a maze pattern cannot be made with a closed maze when the stimulus is intense enough to produce some convulsions.

Qualitative Results

Preceding auditory stimulation, all animals of the control and the experimental groups had no difficulty in learning the maze. The animals readily ran through the tunnel and ate their food on the feeding stand.

The performance of the rats following auditory stimulation showed marked differences between those animals which had had a convulsion and those that had not. When placed at the starting point, the nonconvulsive animals proceeded directly toward food as they had previous to auditory stimulation. They were in no way inhibited by the tunnel. On the other hand, seven of the convulsive animals, when placed at the starting point, ran toward the tunnel and remained there. After being in the tunnel for 10 min., the animals were removed, given a 2-min. rest period, and then brought back for an additional trial. For each of the three retest trials, their behavior was the same, and at no time did they venture upon the feeding platform to eat. The two remaining animals of the seizure group sought shelter before they sought food. Both remained in the tunnel for 10 min. on their first retest trial. One of them remained in the tunnel for another 10 min. on its second retest trial. When given the third retest trial, this animal, after spending some time in the tunnel, walked to the feeding platform and ate. The other animal on its second and third retest trials did not stop in the tunnel but proceeded to go through and eat upon the open feeding stand.

As a final argument it can be pointed out that at the choice point the tunnel on either arm was the same distance away. Yet the convulsive animal turned without hesitation toward that shelter which was located on the correct pathway to the food.

We would not agree entirely with Griffiths that the animal which is "excited emotionally" by auditory stimulation takes advantage of any shelter in the field. Only the convulsive rats seek such shelter. Neither do our results indicate that auditory stimulation facilitates maze behavior. The evidence of our results supports the view that the accelerated speed on the open maze in the rats of Griffiths' study was due to a desire to obtain shelter which was supplied by the enclosed food box.

CONCLUSIONS

The findings presented in this study indicate the following conclusions:

1. Auditory stimulation which does not produce seizures, affects neither time nor error scores.

2. Neither auditory stimulation nor convulsions destroys the memory traces of the maze as indicated by number of errors made during last three retest trials of the experimental group.

3. Marked differences in time scores are observed between convulsive animals and both nonconvulsive and control animals. The convulsive group takes a significantly longer time to complete the maze than either the nonconvulsive or control group. This behavior, the authors believe, is the result of fear, which causes the animal to seek shelter instead of food.

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ANOXIC AND CONVULSIVE AMNESIA IN RATS

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It is generally presumed that the amnesia produced by electroconvulsive shock (ECS) in human patients and experimental animals is the result of brain damage or dysfunction caused by the convulsion. The purpose of the present experiment was to determine whether similar behavioral effects could be produced by anoxia—a type of treatment which is known to be capable of causing damage or dysfunction of the kind presumably involved in ECS.

Some similarity in the mechanisms of these two types of treatment is suggested by the fact that young animals are more resistant than older ones to the effects of both anoxia (2, pp. 175, 190) and ECS (1, p. 51).

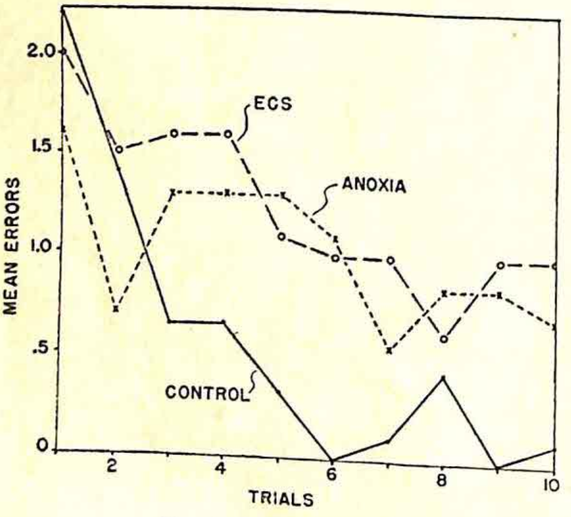

FIG. 1. Learning curves

METHOD

The general method was essentially that employed in an earlier study (1). After preliminary runway training, 24 male albino rats (130 to 190 gm.) were given one trial per day for ten days, in a three-choice-point alley T maze, with trap doors just before each choice point. They were motivated by 23 hr. of food deprivation, and the goal box contained moist food. Eight of the rats were assigned to the ECS group, 7 to the anoxia group, and 9 served as normal controls.

ECS and anoxia treatments were given concurrently with the maze training—a treatment 1 hr. after each day's trial, so that any resultant amnesia might affect what had been learned on that day.

Grand mal convulsions were produced by approximately 50 Ma. of 60-cycle current, applied through ear-clip electrodes, for ¼ sec. Anoxia was produced by manual compression of the rat's chest, which was continued until the rat became limp and motionless—usually about 1 min.

Two days after the last treatment, the rats were killed and the brains prepared for histological examination.

RESULTS

The immediate effects of the two types of treatment were very similar. In both cases, as consciousness appeared to return, there was a period of catalepsy lasting several minutes, and accompanied by exaggerated startle reflexes. During the next half hour the rats were relatively inactive, with the startle reflex slowly returning to normal.

Figure 1 shows the average learning curves for the three groups. These curves are much like those found previously for ECS with rats of this size (1, p. 52).

On the basis of previous work (1) trials 6 through 10 were chosen for statistical analysis. The mean errors per rat during this period (with standard errors of the means) were: control, .67 ± .24; anoxia, 4.0 ± 1.0; ECS, 4.6 ± .82. The two experimental-group scores are insignificantly different from each other, but they both differ from the control-group score at better than the .01 level of significance.

Histological examination revealed no clear evidence of brain damage in any of the groups. This result must be considered inconclusive rather than negative, for it is possible that slight damage in the experimental groups may have been masked by the very great intragroup variability. Statistical treatment of cell counts was not attempted.

DISCUSSION

Since anoxia appears to produce much the same behavioral effect as ECS, it may deserve consideration as an alternate procedure in both experimental and therapeutic applications. It has at least two potential advantages:

(*a*) Unlike electrically induced convulsions, anoxia can be produced under anesthesia, eliminating the unpleasantness of the treatment. (*b*) Whereas the grand mal convulsion is an all-or-none affair, the intensity of the individual anoxia treatment can be varied over a wide range—presumably with an accompanying variation in the amount of amnesia produced.

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PROPRIOCEPTIVE INFLOW AND SUSCEPTIBILITY TO EXPERIMENTALLY INDUCED SEIZURES[1]

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"Sound-induced" seizures are still a scientific enigma. Despite the label, their etiology, and the contribution of auditory stimulation to it, are almost exclusively matters of speculation. Several facts, however, stand out rather clearly: (*a*) Most investigators agree upon the presence of sound as a condition requisite to seizure induction; (*b*) the epileptoid phase is, if it occurs, invariably preceded by a period of intense bodily activity; (*c*) not all animals can be made to display the seizure pattern; (*d*) seizure sensitivity can be altered by dietary regulation, the administration of drugs, and, quite probably, by vagotomy and surgical insult to the frontal lobes (2). From these conclusions may be drawn the inference that the "audiogenic" attack represents an inability of certain animal subjects, i.e., those with defective "governor mechanisms," to compensate for a marked, and perhaps sudden, increase in level of sensory inflow. This critical increase may be provided solely by auditory input, or it may result from certain intraorganismic changes provoked by auditory excitation: positive feedback from the viscera and/or the proprioceptive end organs. It may also, of course, be effected by a combination of excitation from each of these several sources.

There are no data which yield the confident deduction that seizures are exclusively determined by auditory input. There is, in contrast, considerable evidence to indicate that auditory input may serve a *detonator function*, setting off other activity that in turn contributes significantly to the occurrence of the convulsive response. The importance of visceral processes is indicated by the enhancement of seizure susceptibility with "emotional upset" (10) and its decrease subsequent to vagotomy (8) and frontal ablation (15). The importance of vestibular activity is suggested by the violent running and circling movements which precede the tonic-clonic episode, the depression of the righting reflex in the postconvulsive period, and the increase in seizures which follows rotation (5). Finally, the importance of proprioceptive excitation from the voluntary musculature may be inferred from the inevitable presence of the running phase in the seizure pattern, the decrease in latency of the first running attack with increase in the area of free movement (12), and the reduction in susceptibility achieved through binding *S* (11) or forcing it to exercise during exposure to test conditions (9).

The present experiment was an attempt to obtain more direct evidence of the contribution of the last-mentioned processes (kinesthetic) to the induction of the convulsive reaction through a comparison of seizure sensitivity in unoperated animals and that in animals subjected to sectioning of the dorsal funiculus and vestibular deafferentation. Inability to devise a surgical technique for effecting vestibular deactivation without injury to the auditory mechanism, however, necessitated restricting the comparison to unoperated *S*s and those with spinal injury (the adroit solution to this difficulty used by Finger, Bice, and Day [3] appeared in the literature while this paper was in preparation). Accordingly, from the general hypothesis stated in the first paragraph certain more specific predictions have been derived:

1. If proprioceptive stimulation from the voluntary musculature constitutes an important source of convulsion-inducing feedback, interruption of the major proprioceptive pathways from the trunk and limbs may be expected to result in cessation of the seizure response or a diminution in its frequency and/or intensity—the latter alternative being reflected as an increase in the number of terminal running as compared with full convulsive attacks. In addition, if proprioceptive feedback is important in initiating the running phase itself, the latency of the first running

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[1] Supported by a grant from the Carnegie Foundation administered through the University Center in Georgia.

attack may be expected to be longer in the operated animals.

2. If the influence of proprioceptive feedback is of more limited proportions so that the above changes do not occur, its contribution may still be seen in the increased latency of the tonic-clonic sequence, the increased duration of the running phase, and the increased frequency of the running attacks.

METHOD

Design

The experimental design involves the use of white rats which were exposed to an arbitrary number of auditory tests, then divided into two equivalent groups based on the frequency of nonreactions, running attacks, and full convulsions secured from each animal. One group, the E group, suffered bilateral dorsal hemisectioning performed at the cervical level; the other, the C group, with the exception of surgery, received the same treatment as E. After operative recovery of the E animals, both groups were subjected to a further series of tests and compared on the several indices of seizure sensitivity.

Subjects and Apparatus

Twenty-four Sprague-Dawley males 50 days of age at initial testing served as *S*s. Each was placed in an individual cage at 30 days and housed in this fashion throughout the experiment.

A sound-resistant test chamber was devised by enclosing a small (17-in. diameter and 10-in. depth) galvanized metal tub, painted flat black, in a cork-lined wooden box fitted at the top with a hinged observation window. Auditory stimulation was supplied by a 4-in. doorbell mounted at the top center of the tub. Stimulus intensity was relatively constant throughout the chamber; measurements made at the floor center and four points on the perimeter (ten determinations at each position) with a GRC sound-level meter yielded a mean of 97.5 db. with a range of 90 to 99 db. Stimulus duration was controlled by means of a G. E. Model T-48 interval timer. Each animal was tested in a wire-mesh cage, 9½ in. in diameter and 6¾ in. deep, placed about 1 in. from the bell. The *S*s' reactions were clocked with a Meylan stop watch.

Procedure

Test sequences. Each *S* received a total of 33 tests, comprising three test sequences. Test Sequence I, 5 daily 1-min. exposures to the bell, was conducted to provide data for formation of the experimental groups. When no positive reactions, either running or full convulsions, were obtained, this sequence was terminated and all animals submitted to dietary regulation to enhance seizure susceptibility. After four days of ad libitum feeding of a magnesium-deficient diet, Test Sequence II was begun. It consisted of 6, 1-min. and 2, 2-min. tests conducted on alternate days. At the end of this sequence, E and C groups were created and the inadequate diet replaced by standard laboratory chow. After two weeks to permit recovery from the effects of the dietary regimen, the E group was subjected to spinal transection. Sutures were removed seven to nine days later, and all animals were again placed upon the special diet. In another four days Test Sequence III, 7, 1-min. and 13, 2-min. tests spaced at 48-hr. intervals, was begun.

Diet. The mildly deficient diet used to enhance seizure sensitivity is similar to that used by Patton and Lazovik (13) in their experiment on sensory preconditioning. It consisted of the following constituents: sucrose, 63 per cent; casein (pure), 18 per cent; fat (Crisco), 5 per cent; salt mixture from which the $MgSO_4$ had been omitted, 4 per cent; vitamin mixture, 10 per cent. (The salt mixture, prepared from a modification of the Hawk and Oser formula, contains all minerals, with the exception of magnesium, known to be required. The vitamin mixture, prepared by General Biochemicals, Inc., Chagrin Falls, Ohio, includes adequate amounts of both fat-soluble and water-soluble vitamins. The composition of these mixtures may be had upon request.) No provision was made to eliminate more magnesium from the *S*'s intake than that omitted from the salt mixture.

Surgical procedure. The surgical procedure employed in the present experiment is similar to that previously utilized by Lashley and Ball (7). The *S* was placed under sodium pentobarbital anesthesia, supplemented when necessary by ether; the skin in the dorsal cervical region was shaved, wiped with tincture of iodine, and a skin incision made. The muscles were next separated in the mid-dorsal line by blunt dissection and the neural arch of one of the cervical vertebrae removed with bone forceps. Usually the third cervical vertebra was selected, but in several animals the first or second was ablated. Bleeding was controlled by sponges and, in extreme instances, by cautery. A transverse incision was made in the dura and the cord exposed. Then a fine cautery needle, passed from side to side through the cord at the intended lesion depth, was lifted, cutting and cauterizing the cord. The wound was sutured and dressed with collodion. The animals recovered quickly, with no apparent postoperative complications, the skin sutures, as previously indicated, being removed from seven to nine days after operation.

Testing procedure. All tests were conducted as individual tests. Except where it was necessary to terminate stimulation to prevent possible loss of *S* (two animals died in convulsion during Sequence II and had to be replaced), the duration of the tests was that specified above. Stimulation was applied after a 30-sec. observation of the *S*'s reactions in the test cage. A check list was kept of the usual symptoms displayed in prestimulation, preconvulsion, convulsion, and postconvulsion periods, and notes were made of any unusual features of behavior. Latencies for the first running attack and the epileptoid phase as well as the number of running attacks were also recorded. At the end of each test, the *S*'s response was rated on a three-point scale (NRC). If the animal failed to display vigorous, apparently blind, running and darting for a continuous period of at least 3 sec., its behavior was classed as *nonreaction* (N). If running occurred, the test was scored "R." The running response (R) was usually presaged by weaving of the head and body, mincing gait, backward circling, and sidling movements. These were replaced almost immediately by violent gyrations of sometimes extremely high velocity. If running culminated in a tonic-clonic episode, the response was designated convulsive (C). During these last mentioned attacks, which were usually of an extremely severe sort, the animal clung to the side of the cage or fell on its side or back. As in other instances of seizure in magnesium-deficient animals (13), the tonic phase tended to be predominant.

Further description of measures used and their evaluation. The E and C groups were organized at the end of Sequence II by matching pairs according to the number of N, R, and C responses displayed by each *S*. Table 1 presents the total N, R, and C responses for the two groups.[2] The adequacy of this match was checked by performing a chi-square test upon the totals of the various categories for both groups, the expected frequencies being derived from the marginal totals. The resultant composite χ^2 was clearly not significant ($\chi^2 = .48$, $df = 2$, $p < .80$). It was realized, meanwhile, that this application of chi square may be questioned, for the assumptions of independence and randomness of selection were not met; i.e., the frequencies entered into the cells of the contingency table represented, not the results of one test performed on 192 cases selected at random from a population, but of eight observations on each member of 12 matched pairs. Inspection of the matching, however, inclines the writers to accept the χ^2 evaluation as valid.

TABLE 1

Total Responses on Pre- and Postoperative Test Sequences and Mean Frequency and Intensity Scores

GROUP	TEST SEQUENCE II (8 tests)					TEST SEQUENCE III (20 tests)				
	N	R	C	Mean F	Mean I	N	R	C	Mean F	Mean I
Control	79	6	11	.18	.82	180	13	47	.25	.89
Experimental	77	5	14	.20	.87	168	27	45	.30	.81

Nonetheless, in order to meet the objections just raised and to cast the data in a form in which, in the appraisal of group trends, the contributions of the individual *S*s are given equal weight and formal cognizance, two responsiveness scores, the F score and the I score, were derived. The F score is a relative frequency score; it is computed by dividing the number of R and C reactions by the total number of tests. The I or intensity score is slightly more complex. Its calculation requires making the assumption that N, R, and C represent three equally spaced points on an interval scale: N and C the extremes, R the mid-point. Thus, if N has a weight of 0 (no responsiveness) and C of 1.00 (maximum responsiveness), R assumes a weight of .50, and I is computed by summing the weighted R and C scores and dividing by the number of R and C reactions.

Additional indices of sensitivity are defined as follows: The *latency of the first running attack* is the time in seconds from onset of stimulation to the first appearance of vigorous running. To be classed as vigorous, running, which usually follows a circular path, must be at least 3 sec. in duration and involve movement over the path twice through 360° from the region of initiation. The *latency of the epileptoid phase* represents the interval between activation of the bell and the unequivocal presence of an epileptoid sequence. This last is judged to have occurred when *S*, usually first having displayed widespread hypertonus, falls upon its back or side and convulses. The *mean duration of running prior to convulsion* represents the sum of the durations of the individual running attacks for each animal on tests ending in a tonic-clonic episode divided by the number of tests on which convulsions were obtained. The *mean number of running attacks* prior to convulsion is computed by dividing the total frequency of running attacks on C tests for each *S* by the number of C tests recorded for that *S*. Finally, the *relative duration of running* is secured by dividing the sum of the durations of the individual running attacks on the C tests for each animal by the mean latency of the epileptoid phase for that animal. (It is realized that the representativeness of the individual mean scores upon which the data in Table 2 are based are subject to challenge, for they are derived from samples of unequal size, the underlying distributions of which cannot be specified. Median scores were computed, however, and compared with the means; the high degree of similarity noted between these two estimates of central tendency prompts the writers' confidence in the reliability of the means and hence the legitimacy of their use.)

Wilcoxon's Matched Pairs Signed Ranks Test (16) was employed in the evaluation of all between-groups comparisons made upon the data of this experiment.

RESULTS

Frequency of response: the F score. The first hypothesis predicts cessation, or reduction in frequency, of seizure responses in operated rats. Statistical analysis of the F scores of the C and E groups reveals no significant difference ($p > .05$).

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[2] Individual matching data are included in Table I. This table and Table II, which also presents individual test results, are available by ordering Document 3951 from American Documentation Institute, Auxiliary Publications Project, Photoduplication Service, % Library of Congress, Washington 25, D.C., remitting $1.25 for microfilm (images 1 in. high on standard 35-mm. motion picture film) or $1.25 for photocopies readable without optical aid.

Severity of response: the I score. Hypothesis 1 also predicts that reactions secured from the operated group will be less severe. Pair-by-pair comparison reveals that in 6 of the 12 cases C > E. These differences, however, for the most part are small, and there is one striking negative case. Statistical treatment reveals no significant between-groups difference ($p > .05$), but suggests further experimental evaluation with larger groups and, perhaps, a greater number of tests.

Readiness of response: latency and duration scores. Table 2 presents medians and ranges of the various latency and duration scores (individual data are filed with ADI. See footnote 2). No difference obtains between the groups for latency of the first running attack ($p < .05$). It appears that afferent excitation relayed via the dorsal funiculus exerts no apparent influence upon the induction of the running phase, thus has no relevance for the convulsive sequence prior to this period. Meanwhile, the story is a different one for the period subsequent to the initiation of running: The latency of the epileptoid phase is unequivocally longer in the operated animals ($p < .03$), implying that interference with the functional integrity of the dorsal funiculus *does* influence the character of the seizure reaction. A greater amount of preconvulsion activity is required to bring about the epileptoid sequence in the surgically treated *S*s: There are, on the average, more running attacks in E prior to convulsion ($p < .01$); there is longer duration of running ($p < .01$); a greater proportion of the interval between first running attack and convulsion is devoted to running ($p < .05$). Thus, while the initial hypothesis of this experiment does not receive support, its alternative, Hypothesis 2, appears to be confirmed in all its aspects. In addition, while no attempt was made to scale the severity of the tonic-clonic episodes, the general impression gained was that they were less intense and of shorter duration in the E group.

Evaluation of operative lesions. Upon completion of test Sequence III the E animals were sacrificed, and a portion of each cord extending several segments on either side of the lesion prepared as serial sections for evaluation of the extent of damage. The sections were stained in haematoxylin and eosin. While this staining technique does not reveal nerve fibers in detail, it does make possible a reliable estimate of the depth of penetration of the individual lesions.

The results of surgical insult are diagrammatically summarized in Figure 1. Inspection of the representative cross sections in the upper row indicates three depths of lesion: I, found in one animal (no. 12), involves only superficial damage to *fasciculus gracilis* and *fasciculus cuneatus*; II, found in four animals (no. 16, 20, 22, 30), represents somewhat deeper penetration involving the dorsal horn; III, found in four animals (no. 21, 28, 29, 32), includes considerably more damage than II to the *fasciculus gracilis*, *fasciculus cuneatus*, and the dorsal horn, with sparing of the cerebrospinal tract. In three animals (no. 18, 23, 25) the lesion penetrated at an angle, being deeper on the right side as indicated in the lower row of diagrams.

The histological appearance of the lesions

TABLE 2

Median Scores and Range of Control and Experimental Groups on Additional Indices of Responsiveness during Postoperative Test Sequence (III)

MEASURE	GROUP			
	C		E	
	Mdn	Range	Mdn	Range
Mean latency (in sec.) per trial, 1st running attack	23.8	12–62	28.0	6–52
Mean latency (in sec.) per trial, epileptoid phase	33.8	15–80	68.8	0*–83
Mean duration (in sec.) per trial, running prior to convulsion	5.55	4.0–9.0	13.55	0*–17.5
Mean number running attacks per trial prior to convulsion	1.25	1.0–2.0	1.88	0*–3.0
Mean ratio running to total time per trial prior to convulsion	0.19	0.07–0.26	0.21	0*–0.51

* Two Group E animals (no. 20 and 32) showed no convulsive reactions on Test Sequence III.

was in no way unusual. Scar tissue typically bridged the cut ends, and occasionally small cysts were present. In a few preparations, notably number 25, small unabsorbed clots were observed. While the staining technique utilized could not be expected to provide evidence of neural regeneration, the use of a cautery renders doubtful (cf. 14, pp. 11 ff.) its occurrence in any significant degree.

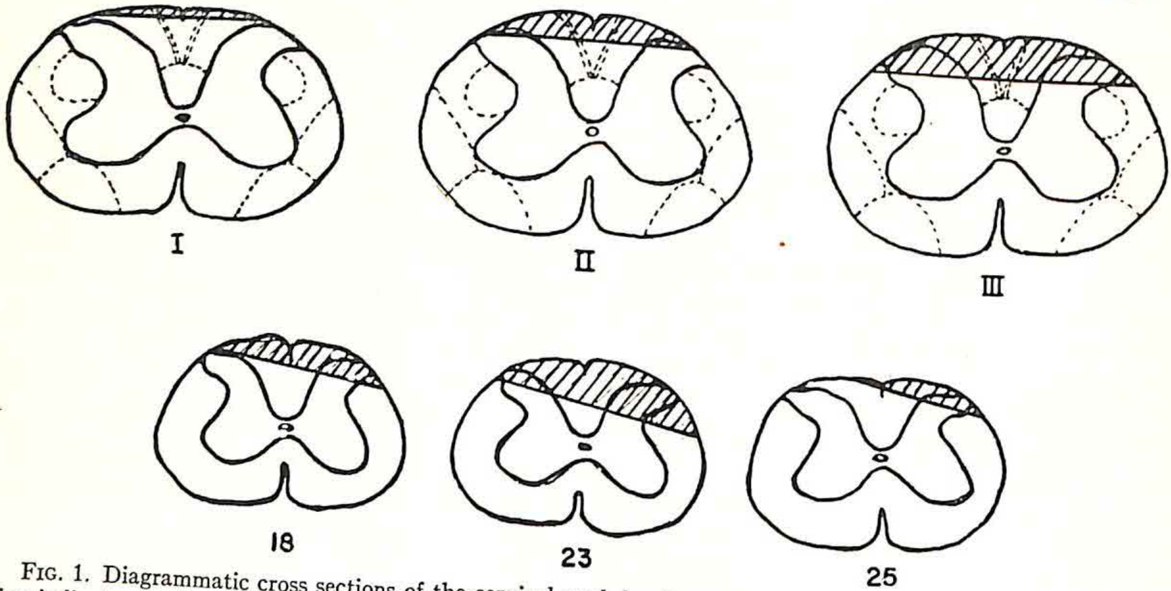

FIG. 1. Diagrammatic cross sections of the cervical cord showing damage suffered by E animals. Shaded portion indicates depth of lesion.

DISCUSSION

The *E*s' major concern, after an over-all consideration of the present data, is directed toward accounting for the limited (in terms of their pre-experiment expectation) contribution of proprioceptive excitation from the voluntary musculature to the character of the seizure response. Speculation may be extended along two lines: (*a*) methodological, i.e., explanation in terms of either inadequate lesions or restrictions inherent in the deactivation approach itself; (*b*) functional, i.e., explanation in terms of the limited functional significance either of the anatomical pathways or the sensory modality under consideration.

It is quite probable that the limited influence attributable to the dorsal root processes results from incomplete experimental lesions, for in no E animal were the dorsal tracts completely severed. Examination of sections from even the most severely injured preparations suggests the possibility of considerable transmission through the uninjured portions of the dorsal funiculus. This possibility is supported by the fact that no locomotor defects were in evidence in the postoperative home-cage behavior of the E group, and by earlier reports (6, 7) of quick locomotor recovery in animals suffering deeper penetration than the present *S*s. Had the dorsal columns been completely severed, conduction may still have been possible, of course, as a result of collateral transmission (6) or regeneration (14). Electrocautery was used in producing the lesions as a precaution against the latter.

In the selection of the present surgical procedure the writers followed the assumption of Lashley and Ball (7) and of Ingebritsen (6) that in the rat, as in vertebrates of higher form, tracts of the dorsal funiculus serve as important avenues of proprioceptive excitation. That these tracts are important to such a function, or for that matter, that they are involved in such a function is, however, still to be empirically established. Meanwhile, previously published data clearly suggest that proprioceptive transmission is, at most, not their exclusive prerogative: Two studies (6, 7) describe only minimal locomotor dysfunction in animals subjected to much deeper dorsal lesions than those of this experiment; Ghiselli (4) in a well-controlled, and Brown (1) in an even more extensively controlled, investigation report normal sensory discrimination by animals with similar lesions in tasks regarded to be dependent upon kinesthetic cues. The results of the present study, in addition, are not inconsonant with such a view. In the absence of physiological data from which to construct confidently a functional map of the rat's spinal cord, future experimentation might at least include the interruption of other tracts conceivably proprioceptive in function (e.g., the spinocerebellar tracts) instead of, or in addition to, the dorsal columns.

An alternative explanation is that proprioception is simply not important for these seizures. This is prompted by Finger, Bice, and Day's (3) recent conclusion that vestibular excitation is irrelevant with regard to seizure incidence. However, the experiment upon which this conclusion is based is not entirely convincing, for it may be objected that the pharmacologically produced vestibular dysfunction described by these workers may have been of insufficient magnitude to effect a noticeable change in susceptibility and/or their behavioral data not extensive enough to reveal it—these last could have included more than a tabulation of the number of animals showing R or C reactions during each test sequence. Finally, even though the limited significance of the vestibular and kinesthetic processes, considered individually, be demonstrated, a further possibility presents itself, i.e., that it is the interaction of these two sources of excitation that is important. This warrants future experimental consideration, as does another still unexamined problem, the manner in which auditory stimulation brings about the running phase of the response sequence.

Two additional observations merit brief mention: one physiological, one behavioral. Flushing of the skin surfaces, with peripheral vasodilation, was the most obvious symptom of magnesium deficiency. It was, however, much more variable than that previously reported (13). It did not appear at the same time in all animals, nor was it always present once it had been observed. It was, furthermore, not correlated to any high degree with the occurrence of convulsions, for animals on certain tests responded in a most extreme fashion while showing no clear signs of vasodilation, on other occasions gave no response even though severely flushed.

Most investigators of audiogenic seizures have ignored or tended to minimize the importance of more complex psychological variables as determinants of the convulsive syndrome. Survey of the protocols of the present subjects on the first few tests suggests the advisability of re-evaluating the role of such variables. Without exception, the animals, which were gentle, tractable, "curious" in the initial test situation, began, after only one or two exposures to the bell, to show premonitory symptoms prior to auditory stimulation—head sway, weaving body movements, preening, scratching, immobile crouching, change in respiratory pattern, piloerection, etc.— and vigorously and loudly to resist being removed from their home cages and placed in the test chamber.

SUMMARY AND CONCLUSIONS

Twelve matched pairs of young male Sprague-Dawley albino rats, maintained on a magnesium-deficient diet, were subjected to 20 auditory tests administered on alternate days, after one member of each pair had suffered damage to the dorsal funiculus at the cervical level. Comparison of the test records of operated and unoperated animals revealed no reliable difference in the frequency or severity of reaction, but the operated *S*s required more time and displayed a greater amount of violent running before reaching full convulsion. Contingent upon the validity of the assumption that the rat's dorsal columns transmit proprioceptive excitation, it may be inferred that proprioceptive inflow is a contributory factor in the production of these experimentally induced epileptoid attacks.

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INCREASED RESISTANCE TO AUDIOGENIC SEIZURE IN RATS TRAINED ON AN INSTRUMENTAL WHEEL-TURNING RESPONSE

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An interesting by-product of the many studies on audiogenic seizure sensitivity in the rat has been the frequent observation that affected animals exhibit various forms of substitute behavior during nonseizure trials (1, 4, 6, 8). Miscellaneous activities such as teeth-chattering, restless head and body movements, nest-building, and nose- and ear-rubbing have often been reported (as reviewed in 3, 14). Seizure apparently seldom ensues if such forms of behavior occur, and this activity has therefore been interpreted as a substitute form of response—or as a means of avoiding convulsion.

Some objective evidence that indirectly supports this hypothesis has been reported. Adding mild shock to sound stimulation was observed to produce more crouching in the rat than results from sound stimulation alone, and was followed by fewer convulsive attacks (2). It has also been reported that convulsive responses were reduced in number when animals were forced to move vigorously during stimulation (5, 10).

Up until the present time, however, there has been no attempt to control the specific type of activity which the animals may use as the substitute response. No direct experimental attack on this problem has been reported. The present experiment was therefore designed to test the hypothesis that training seizure-sensitive animals to make an instrumental wheel-turning response will result in greater resistance to seizure.

METHOD

Subjects

A group of 215 albino rats from 3 to 6 months old was screened for the experiment. Sixty-six of these animals were found to be seizure-sensitive. From this group 22 animals (8 male and 14 female) were selected for the experiment on the basis of a series of equation trials.

For the critical test trials the original 11 pairs of animals were used. Between the fifth and the ninth test trials four animals died, necessitating a reduction to 7 pairs. Since the animals were paired, the loss of any one animal resulted in the discarding of its mate.

The animals were taken from the colony maintained by the department of psychology at the University of Missouri. They were maintained on a standard laboratory diet of Purina Laboratory Chow with unlimited food and water available at all times.

Apparatus

Screening and Equation Trials

A partially soundproofed box which has been previously described (11) was utilized. It contained doors that allowed *E* to place a smaller, two-compartment box within it. The two-compartment box was placed just below an air whistle calibrated to sound at a fundamental frequency of 12,300 cps. An electric clock was connected to the compressor circuit so that a measure of the time the whistle was active could be obtained. Time measures for the different phases of the seizure behavior were recorded by means of a stop watch.

Training and Test Trials

A Mowrer-Miller box (13) was divided into equal parts by a beaverboard partition providing an experimental compartment (side of the apparatus containing the wheel) and a control compartment (side of the apparatus without the wheel). The small wheel (4 in. in diameter) was set in the right end of the compartment 2 in. above the floor. It was turned by vertical movements of the forepaws. As the wheel turned, it broke the circuit and so reduced the effectiveness of the shock. Continued turning of the wheel as an instrumental—shock-reducing—response was thus encouraged. A whistle of 12,300 cps. was placed directly above the partition so that an equal amplitude of sound would be introduced into both compartments. The bar and food tray on the left side of the Mowrer-Miller box were removed, and the hole was covered by a stiff piece of cardboard. The time during which the whistle and grid were active was measured by an electric clock, and the various phases of the convulsions were measured by a stopwatch.

Experimental Design

Screening Procedure

Each animal was given three 2-min. seizure trials in the soundproofed box, one every three days. After each testing session those animals which showed convulsions were placed in separate cages. At the end of the screening trials a total of 66 seizure-sensitive rats had been obtained.

Equation Trials

Five trials per animal were administered in the soundproofed box in order to obtain data as a basis for pairing the 66 seizure-sensitive animals into two equated groups, permitting use of a matched-pair design. The rats were run in pairs, and the whistle was sounded for 2 min. in all cases.

The animals were first equated according to the total number of tonic-clonic convulsions obtained during the five trials. This placed them in six categories: those having 0, 1, 2, 3, 4, and 5 convulsions. The 44 animals with less than 2 convulsions were discarded. The 22 animals in the other categories were further equated on the basis of an arbitrary scoring method similar to one previously reported (12). *Directed running* was scored 1 point; *undirected running*, 2 points; and *tonic-clonic convulsions*, 3 points.

These three phases were typical of audiogenic seizures in rats (3, 14). *Directed running* consisted of low-velocity activity marked by short, erratic runs and by the animal's apparent ability to avoid striking objects or running into walls. *Undirected running* consisted of high-velocity running usually initiated by a characteristic and unmistakable burst of activity. This phase was further marked by the animal's nonavoidance of objects and barriers. *Tonic-clonic convulsions* consisted of tonic contraction of the musculature of the animal's body followed by a rhythmic contraction and relaxation. These phases were so distinct from each other that the *E*s had little difficulty in timing the duration of each.

After the animals had been equated according to the number of tonic-clonic convulsions and seizure scores, they were further equated for seizure latencies.

Training-Test Series

A total of nine training-test series was given. The Group II animals were in the experimental compartment on the second training-test series (reversal). During all other training-test series the Group I animals were on the experimental side of the apparatus.

Training trials. A series of 16 training trials was given prior to each test trial. This number was selected on the basis of the results of a pilot study run to determine such procedural details. The equated animals were placed in the Mowrer-Miller apparatus with one animal on each side of the partition. Each pair of animals received 30-sec. shock trials with the shock set at 300 volts a.c. The shock was used during training trials to insure learning of the wheel-turning response. The animals received 2 trials per day, three times weekly.

Test trials. Approximately 5 min. after the final training trial the animals were tested. They were again placed in the Mowrer-Miller apparatus. During these trials, however, *both* whistle and shock were used. In each case the shock preceded the whistle by an interval of 3 sec. in order to give the animals in the experimental compartment sufficient time to begin making the wheel-turning response before the whistle was introduced. All test trials followed the same procedure, with both whistle and shock on for a period of 90 sec. This length of period was used since it was discovered in the pilot study that trained animals would very often cease making the wheel-turning response toward the end of a 120-sec. period.

The protocols for the test trials contained the latency in seconds of directed running, undirected running, and tonic-clonic convulsions for both groups of animals. Because of the difficulty involved in statistically treating data expressed in proportions, a *resistance-to-attack* measure was devised. Tonic-clonic resistance scores consisted of the number of seconds an animal avoided tonic-clonic convulsion during a 90-sec. test period. If an animal avoided tonic-clonic attack for the entire test period, it was given a tonic-clonic resistance score of 90 sec. On all other occasions the latency for tonic-clonic attack was used as the resistance score. Resistance scores for directed and undirected running were obtained in the same manner.

An accurate record was also kept on the number of clonic head-forepaw attacks exhibited. Such attacks have been previously noted (9, 12). They consisted of a rapid jerking movement of the forepaws and head, and were usually preceded by the directed and undirected phases found in tonic-clonic convulsions.

During all the training and test trials one *E* observed and recorded the behavior of the animals in the experimental compartment. A second *E* observed and recorded the behavior of the animals in the control compartment.[1]

RESULTS

Equation Trials

The groups were equated so that each animal of a given pair had the same number of seizures. In each group, 4 animals had 5 seizures, 2 animals 4 seizures, 3 animals 3 seizures, and the remaining 2 animals had 2 seizures. The mean seizure latencies for the two groups were approximately equal: 46.0 sec. for the Group I animals and 45.6 sec. for the animals in Group II.[2]

Training Trials

Although there was considerable variability during the first few trials of the training series prior to the initial test, most animals reached their peak of performance on the wheel by the tenth trial. When the Group II animals were placed in the experimental compartment for reversal-test training, they reacted much as had the Group I animals. There was variability in performance during the first few trials which soon leveled off as the response was learned. During the training trials prior to the first retest, however, all the Group I animals began the wheel-turning response on the first trials and continued making the response at a high level of proficiency.

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[1] The authors are indebted to Richard A. Thweatt for his assistance in these observations. The first-named author acted as the other experimenter.

[2] The data are available in Table A, which, along with Tables B, C, D, E, F, G, and H, is available by ordering Document 3950 from American Documentation Institute, Auxiliary Publications Project, Photoduplication Service, % Library of Congress, Washington 25, D. C., remitting $1.25 for microfilm (images 1 in. high on standard 35-mm. motion picture film) or $1.25 for photocopies readable without optical aid.

Test Trials

On the initial test the results were as predicted. Only 5 of the Group I (experimental compartment) animals had tonic-clonic attacks, whereas all 11 of the Group II animals showed tonic-clonic attacks. On the reversal test 6 animals in each group had tonic-clonic attacks. These data are shown in Table 1. Corresponding data for the retest trials are given in Table B (see footnote 2).

The matched-*t* test was used to determine the significance of the difference between resistance scores for each behavior phase of the convulsions. Since trials in which none of the behavior phases of convulsion appeared were included as 90-sec. resistance scores, the curves were markedly skewed. For this reason a square-root transformation was performed and homogeneity of variance tested. After transformation the data for both the initial test and the reversal test were found to be homogeneous with respect to variance. The largest F was 1.38 with 2.97 required at the .05 level of confidence.

The difference in tonic-clonic resistance scores for the two groups on the initial test yielded a t of 2.74, significant beyond the .05 level of confidence. The tonic-clonic resistance scores for the two groups on the reversal test were almost identical. These data are in Table 2, and are based upon individual data given in Table C; corresponding means for the remaining test trials are given in Table D (see footnote 2).

The T test as devised by Wilcoxon (15) was also used to test the significance of the difference between the two groups on the initial test trial. This nonparametric test does not require homogeneity or independence, and so the data could be utilized without transformation. The difference between the two groups was found to be significant beyond the .05 level of confidence.

The mean tonic-clonic resistance scores for both groups of animals on all nine test trials are shown in Figure 1. The difference in resistance scores between the two groups was tested for each of the seven retest trials. The difference was found to approach significance only on the second retest trial. This difference yielded a t of 2.05 with 2.29 required for significance at the .05 level of confidence. It will be noted that the curves gradually converged and overlapped on the fifth retest trial. Since the curve for Group I was fairly constant, this convergence was due largely to a reduction in seizure sensitivity on the part of the Group II animals. It will also be noted that the Group I animals showed the lowest tonic-clonic resistance scores on that trial during which they were on the control side of the apparatus.

TABLE 1

Number and Per Cent of Tonic-clonic Attacks on Initial and Reversal Test Trials

TEST TRIAL	N	GROUP I		GROUP II	
		Number of seizures	Per cent seizures	Number of seizures	Per cent seizures
Initial	11	5	45.5	11	100.0
Reversal	11	6	54.5	6	54.5

TABLE 2

Mean Tonic-Clonic Resistance Scores for Initial and Reversal Tests

TEST TRIAL	N	GROUP I		GROUP II		t	p
		Mean	σ_M	Mean	σ_M		
Initial	11	72.1	7.1	39.2	7.6	2.74	.05
Reversal	11	59.6	9.0	59.8	9.7	.10	—

The data obtained on the type of seizure exhibited indicated that there was a steady increase in the number of clonic head-forepaw attacks as the experiment progressed. On the initial test, only 6 per cent of the seizures were of the clonic head-forepaw type. By the seventh retest trial 83 per cent of the convulsions exhibited were of this type. (For data given in Table E see footnote 2.)

There is some evidence to support the view that the wheel-turning response raised tonic-clonic resistance scores even for those animals which did exhibit seizures. For such cases, it was found that the group on the experimental side of the apparatus had higher mean latency scores during all test trials except the reversal, where the mean seizure latencies for the two groups were approximately equal. Although these differences did not approach significance, they were in accord with the hypothesis. The data are given in Table F (see footnote 2).

The resistance-score data (given in Tables G and H, see footnote 2) for directed and undirected running were similar to the results obtained from analyzing tonic-clonic resistance scores. Differences significant at the .05 level of confidence were obtained on the initial test trial.

Qualitative Observations

The animals on the experimental side of the apparatus exhibited a variety of behavior patterns during the test trials. Those animals that managed to avoid seizure usually remained at the wheel during the entire 90 sec. Occasionally, however, an animal would show the typical startle response, leave the wheel for a few seconds and then return to it and continue making the response throughout the remainder of the trial.

On at least eight different occasions animals continued making the wheel-turning response while involved in seizure. In all such cases, however, the animal left the wheel and performed running and jumping responses before returning to it during the convulsion. It was also noted that if one of these animals happened to fall away from the wheel, it would continue making those responses even though they were nonfunctional as far as the wheel was concerned. It was further observed that animals which went into seizure and did not return to the wheel occasionally exhibited spasmodic movements of the forelegs and made

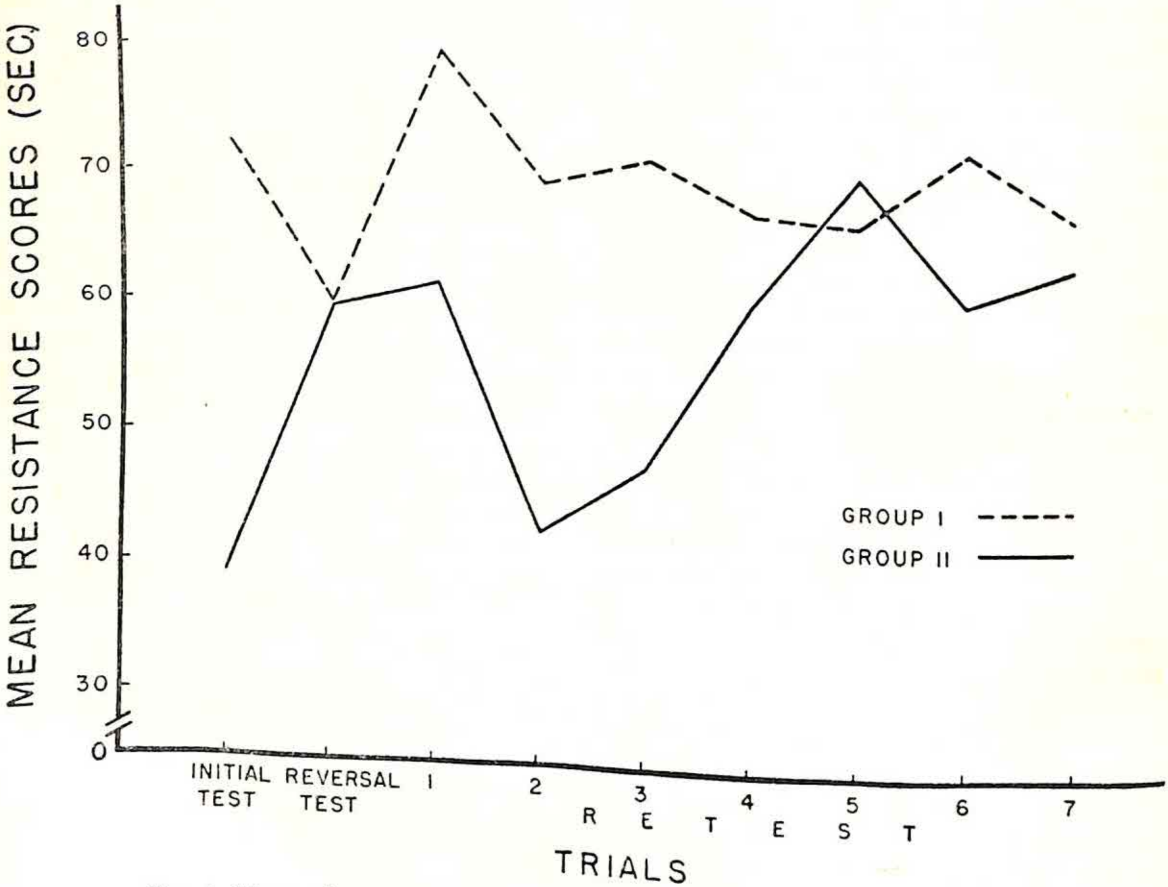

FIG. 1. Mean seizure-resistance scores for both groups on all nine test trials

posturing responses which simulated those performed at the wheel. This behavior was also noted on several occasions in the animals on the control side of the apparatus. Such behavior was not observed, however, unless the animals involved had previously been given wheel training.

DISCUSSION

The results of the experiment support the hypothesis that the opportunity to make a well-learned instrumental response will serve to reduce the effect of high-frequency sound on seizure-sensitive rats. Not only was the difference in tonic-clonic resistance scores between the two groups statistically significant on the initial test trial, but also the resistance scores shifted in the predicted direction during the reversal test. It should be emphasized that this conclusion is based upon results obtained from a direct test of the hypothesis involving (*a*) a specifically trained response, (*b*) individually equated and carefully treated control *S*s, and (*c*) adequate statistical analysis. These conditions were not present in the previous studies from which similar conclusions were drawn.

A problem of interpretation arises from the observation that the tonic-clonic resistance scores were approximately equal on the reversal test. The data offer evidence which may be of importance in explaining this result. The results for the first retest trial show that the tonic-clonic resistance score for Group II was slightly raised over that obtained on the reversal test even though the animals in this group had been returned to the control side of the apparatus for the latter trial. This suggests that wheel training may have had a residual effect which influenced resistance scores for this group even when tested in the control compartment. A similar residual effect may have been responsible for the Group I animals' failure to show lower resistance scores when they were tested in the control compartment. The observation that animals in the control compartment on several occasions exhibited postural and motor responses which simulated those made at the wheel may be offered in support of this hypothesis.

A second problem arises from the finding that the two curves gradually converged and finally overlapped on the fifth retest trial owing to the gradual increase in resistance shown by the Group II animals. It has been found that seizure-sensitive rats apparently undergo a process of adaptation to sound after having been subjected to auditory stimulation many times (5, 9). Such adaptation may have reduced the number of seizures exhibited by the Group II animals during the later trials.

The results are consistent with both the conflict (7) and the pain-threshold-reduction (11) hypotheses. They may also be explained, perhaps more simply, on the basis of antagonism between the wheel-turning response and the responses involved in the initiation of the seizure behavior.

The phenomenon examined in this study may be related to certain problems of more general theoretical significance. For example, it has been a common assumption that human beings often indulge in seemingly irrelevant activity which helps them find partial escape from anxiety-producing situations. This observation seems to parallel the finding in the present experiment that a response learned in one situation may persist as an adjustive mechanism following the addition of a new and presumably prepotent stimulus factor. The relationship between these phenomena and those ordinarily subsumed under the rubric transfer of training becomes evident when account is taken of the modification of the second (test) situation by the addition of such powerful new stimulus components.

SUMMARY

Two groups of rats equated for audiogenic-seizure sensitivity were used to determine whether a well-learned instrumental response would prove effective in increasing resistance to seizures. The animals were trained and tested in a modified Mowrer-Miller apparatus containing a compressor-activated whistle and divided into two compartments by a beaverboard partition. Two primary sets of training-test series were run. On the initial series the Group I animals were trained and tested at the wheel with the Group II animals in the other compartment. Shock was used during training trials to insure the learning of the wheel-turning (shock-reducing) response, and *both* shock and whistle were used during the test trial. On the reversal series the same procedure was followed except that the Group II animals were trained and tested at the wheel while the Group I animals were in the control compartment. During a series of retest trials the Group I animals were again trained and tested at the wheel with the Group II animals in the control compartment.

For the statistical analysis of the data a resistance-to-seizure score was utilized. A tonic-clonic resistance score consisted of the number of seconds during which an animal avoided tonic-clonic attack. Those animals which avoided tonic-clonic attack during a test trial were given a resistance score of 90 sec.

The results supported the hypothesis that opportunity to make a well-learned instrumental response would increase resistance to seizure. On the initial test the difference in tonic-clonic resistance scores between the two groups was significant at the .05 level of confidence with the Group I animals (experimental compartment) showing the higher scores. On the reversal test the resistance scores shifted as predicted by the hypothesis. Implications of the results were discussed.

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THE INFLUENCE OF AREA AND ARRANGEMENT ON VISUAL PATTERN DISCRIMINATION BY MONKEYS[1]

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Men, chimpanzees, and monkeys, and presumably subprimate forms, show improvement from problem to problem when series of problems belonging to a single general class are learned. This learning to learn, or transfer from problem to problem, has been called "formation of learning sets" by Harlow (8) and can be demonstrated to be a highly orderly, predictable process as long as controls are maintained over the experience of the *S*s and the difficulty of the problems.

Monkeys form such efficient learning sets that they eventually come to solve in a single trial a variety of problems involving the discrimination of stimuli differing in many dimensions (8, 13, 14). Little data exist, however, concerning the nature and efficiency of learning sets for discrimination problems of presumably greater difficulty, discrimination between stimuli differing in a single dimension and discrimination between pattern stimuli, i.e., stimuli whose surfaces are partly identical and partly differential. Does stimulus difficulty fundamentally alter the nature and form of learning sets, or conceivably prevent their formation altogether?

There already exists a considerable body of data concerning factors related to discrimination-problem difficulty. Color stimuli are more easily differentiated than those differing in form and size, and patterns are much less easily discriminated than are pairs of objects, either planometric or stereometric, whose total surfaces or contours differ in one or more dimensions.

Whether or not the differential discriminability of different classes of objects is minimized or enhanced by prolonged (learning-set) training remains unsolved. Harlow, in his systematic studies of pattern discrimination, noted that "the differences in discriminability between these two kinds of perceptions [stereometric objects and patterns] appear to be inversely related to experience; differences are greatest in the naive animal and tend to diminish with intensive training" (6, p. 9) and that the initial differences between large and small patterns disappear with training.

On the other hand, subsequent studies by Harlow (7), Meyer and Harlow (15), and Warren and Harlow (19) showed that stimuli differing in color, size, and form were discriminated with differential success and that the differences in discriminability among these cues seemed permanent and not reducible by training.

The problems attacked in the following series of studies bear directly on Hebb's (10) behavioral and neurological theories of behavior. Hebb's description of perceptual acquisition stresses the role of learning. The theory implies that learning should decrease differences in perceptual difficulty, but it does not indicate the nature of the limits imposed by this variable upon facile learning-set formation. Hebb's theory explicitly states that the slow primary learning, which consists of the elaboration of cell assemblies and phase sequences, is not confined to childhood or to the period immediately following recovery from the effects of sensory deprivation. Even with adult primates reared in a normal environment it is reasonable to suppose that the less familiar the task to be performed, the more important slow-increment learning becomes. Once unfamiliar perceptions become familiar, immediate and essentially conceptual "later" learning may be expected to occur. This type of learning amounts to a strengthening of facilitations between cell assemblies and phase sequences that are elaborated during the period of slow primary learning, when connections are set up between wholly unrelated activities.

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[1] This experiment is part of a dissertation conducted under the direction of Professor Harry F. Harlow and submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology at the University of Wisconsin in 1953.

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Hebb comments, regarding the studies of the formation of learning sets, "Harlow's whole argument, showing how the learning capacity may be changed out of all recognition by prolonged experience, is a powerful reinforcement of the position adopted in these pages" (10, p. 114). This would indicate that the following predictions are implicit in Hebb's thesis: Pattern discrimination is a difficult and unfamiliar task for monkeys, and small patterns are, for untrained animals, less discriminable than large patterns. Primary learning will occur in this situation, and its effects will be such that, over a period of many days, a significant improvement in performance will be observed, and after completion of a slow primary-learning phase discriminations of large and small figures will be solved insightfully.

There is a wealth of data demonstrating that differential color is the most effective single cue to efficient discrimination learning by monkeys (see 7, 19). There are, however, a few data indicating how other variables may influence color discrimination, and it is the purpose of the first experiment of this series to determine the role of two such variables: (*a*) area and (*b*) positional arrangement of the differential color areas.

METHOD

Subjects

Eight young rhesus monkeys (animals no. 156, 157, 158, 159, 160, 161, 162, and 164) served as *S*s in this experiment. Their previous experimental experience was limited to 57 days' testing on random planometric-object and stereometric-object discriminations (9). This group of monkeys had been given no previous training on pattern-discrimination problems.

Apparatus

The basic equipment was the Wisconsin General Test Apparatus (8, Fig. 1), which consists of a restraining cage, an adjacent table, and a superstructure that supports opaque and one-way vision screens. Mounted on the table is a movable tray in which there are two food wells spaced 12 in. apart.

The stimuli were made by mounting figures cut from colored construction paper (varying in saturation, brightness, and hue) on 3-in. squares of heavy white posterboard. These stimuli varied in three dimensions: area, positional arrangement, and color. The four colored areas used were 2.25, 4.50, 6.75, and 9.00 sq. in., and these figures occupied 25, 50, 75, and 100 per cent of the background squares. Each of the three smaller areas appeared in three different positional arrangements.

The positional arrangements chosen produce quantitative variation in the amount of the border of the cards which is differentially colored (Fig. 1), and the arrangements are defined in this manner: In one arrangement (TB) the total border of the card is colored; in another (PB), part of the border of each card is colored; in the third arrangement (NB), none of the border of the card is colored.

Each of the ten combinations of the area and positional-arrangement variables was prepared in ten different colors: orange, red, black, yellow, chartreuse, brown, blue, green, purple, and gray. Thus, there was a total of 100 different stimuli. Inasmuch as ten colors taken two at a time yield 45 paired comparisons within any area–positional-arrangement combination, it was possible to generate 450 problems involving color discriminations between stimuli which were alike in area and positional arrangement.

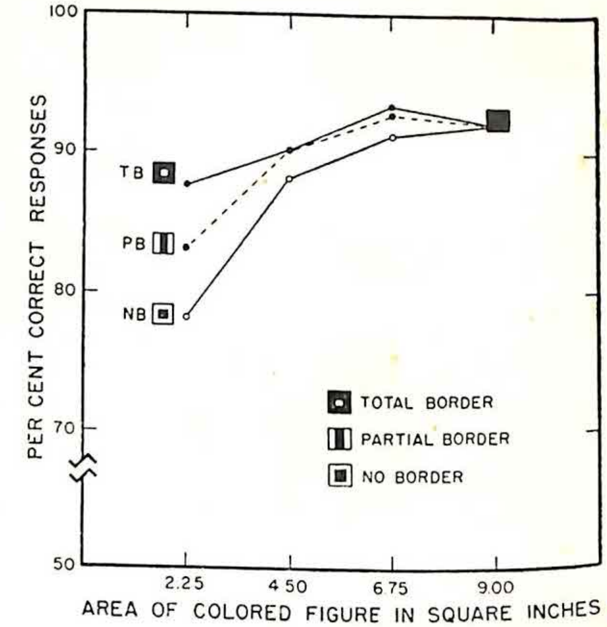

FIG. 1. Performance as a function of area of the colored figure

Procedure

A test trial began with the forward opaque screen lowered in front of *S*. A raisin or peanut was placed in one of the food wells, and simultaneously the baited and empty wells were appropriately covered by the (+) and (−) cards. The one-way vision screen was lowered, the forward screen raised, the tray pushed forward, and *S* was permitted to choose.

Each discrimination problem consisted of ten trials with a pair of cards differing in color only. Ten problems, i.e., one pair of stimuli within each of the area–positional-arrangement combinations, were tested on each day. The 45 paired comparisons were made orthogonal to the ten stimulus categories. Therefore, the experiment lasted 45 days, and scores for each *S* were obtained on a total of 450 discrimination problems. Comparisons involving the same two colors were never tested twice on the same day, and the (+) and (−) colors were randomly altered from pair to pair so that interproblem transfer might be minimized.

Experimental Design

A simple 3 (configurations) by 3 (sizes) by 8 (*S*s) factorial design was used. The 9.00-sq. in. size was omitted because it could not be orthogonal to positional arrangement. As mentioned under *Procedure*, the stimulus categories were all orthogonal to color comparisons, and the possibility of interproblem transfer was minimized so that the analysis of variance provides a meaningful test of the significance of configuration and areas.

TABLE 1

Summary of Analysis of Variance

SOURCE	*df*	SUM OF SQUARES	MEAN SQUARE	*F*
Monkeys	7	12495.78	1785.11	3.188*
Configuration	2	4627.53	2313.76	4.133†
Area	2	18180.36	9090.18	16.238‡
M × C	14	1450.47	103.61	1/5.403
M × A	14	1499.07	107.08	1/5.228
C × A	4	2407.14	601.78	1.075
M × C × A	28	1576.43	559.80	
Total.........	71	42177.78		

* .05 CL.
† .01 CL.
‡ .001 CL.

The variance due to successive testing days was unavoidably confounded with the stimulus-categories by color-comparisons interaction, and so it was impossible to obtain an unequivocal measure of interproblem learning within any area-configuration combination by any means short of a 45-day replication. An estimate of interproblem learning was obtained by comparing total errors (summed over all categories) on successive 9-day periods. The latin square used to render the ten stimulus categories orthogonal to the color comparisons insured that each of the 45 comparisons appeared twice within these 9-day blocks. Meaningful comparisons of the intraproblem learning within any of the categories were possible because each of the 45 paired comparisons occurred once within each category.

RESULTS

Performance, as measured by the percentage of correct discriminations on trials 2 to 10, is plotted in Figure 1 as a function of the differentially colored area, with positional arrangement as a parameter. It is apparent that increases in area up to 75 per cent result in improved discrimination, but the increase from 75 to 100 per cent has little effect on performance. The total-border (TB) arrangement is superior to both the partial-border (PB) and no-border (NB) arrangement, and the PB arrangement is, in turn, more discriminable than the NB arrangement. The magnitude of the differences between the configurations decreases for the larger areas, the differences between the TB and NB arrangements decreasing from 9.5 per cent at 25 per cent to 1.5 per cent at 75 per cent.

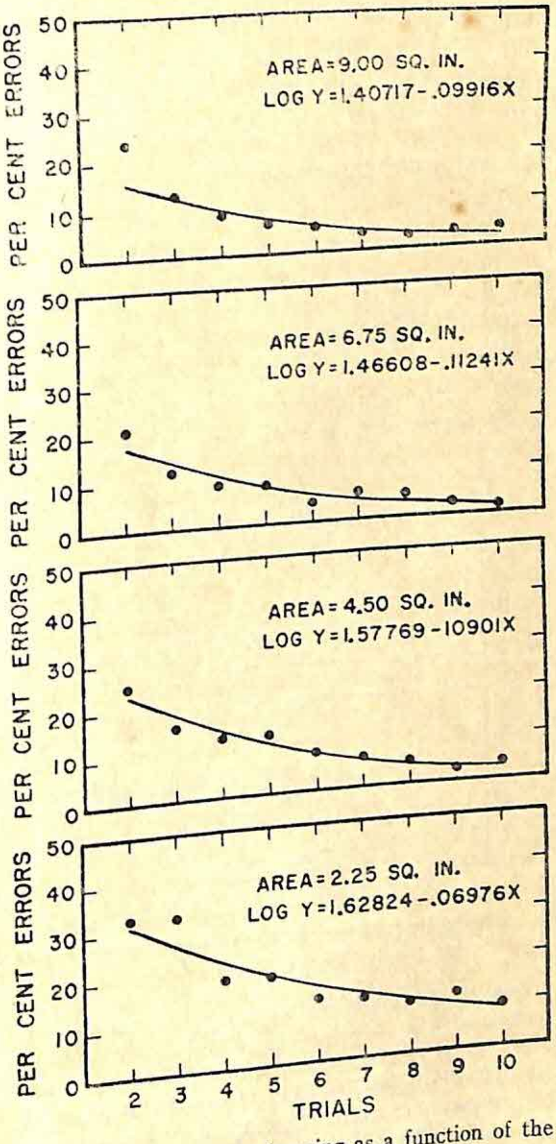

FIG. 2. Intraproblem learning as a function of the area of the colored differentiae

Analysis of variance, summarized in Table 1, indicates that the variations resulting from positional arrangement and from area are significant at the 5 and at the 1 per cent levels of confidence, respectively. The t's of related measures show that fewer total errors were made on the TB arrangement than on either PB or NB, and fewer errors were made on PB than NB. The differences in all comparisons were significant at or beyond the .02 level. Summing over all categories, it is found that more errors were made on each of the two smaller areas than on either of the larger, and the differences are significant at or beyond the .01 level. The increase in correct responses between 25 and 50 per cent differential colored area is significant ($p < .01$); the difference between the 75 and 100 per cent differential colored area is not significant.

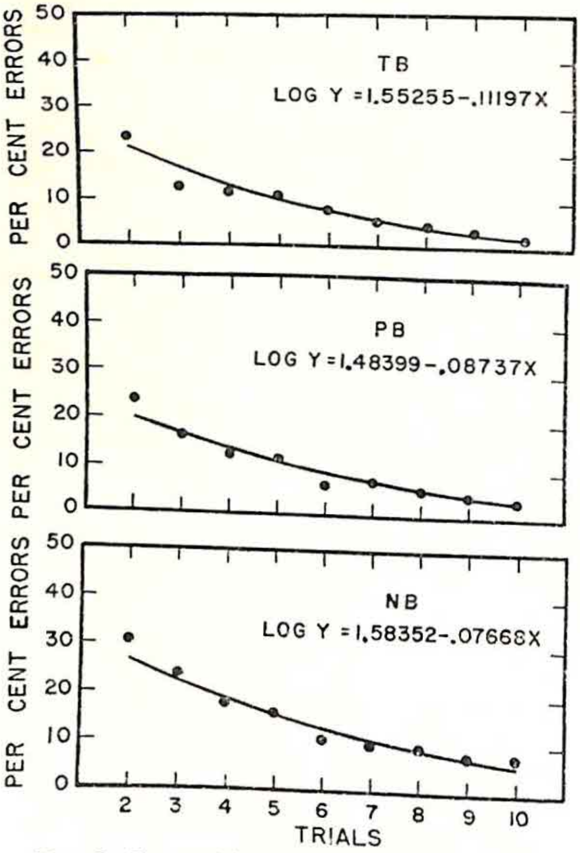

FIG. 3. Intraproblem learning as a function of configuration

The total errors on all categories showed a consistent decrease between successive blocks of 90 problems, but the decrease was not statistically significant at the .05 confidence level. Thus, the data are inconclusive regarding the existence or the magnitude of interproblem learning.

Intraproblem learning as a function of the area of the colored differentiae is plotted in Figure 2 and as a function of configuration in Figure 3. Both figures give the empirical values and the least-square solutions of the general equation $Y = 10^a - 10^{bx}$, for errors on trials 2 through 10.

Comparison of the least-square solutions for each of the four areas and three positional arrangements reveals that these functions differ in slope and asymptote. The curve which best fits the 25 per cent-area data has a much lower slope constant and higher asymptote than the curves fitted to the data obtained in problems involving the larger areas. It appears, indeed, that even after a very large number of trials, the errors in discriminating 25 per cent areas would exceed those made on problems with the larger areas. The NB positional arrangement has a lower rate than the PB and TB curves, but at trial 10 there are no large differences in asymptote among the positional arrangements.

DISCUSSION

The results of this experiment constitute a demonstration of the fact that sensory acuity is a necessary but not sufficient condition for complex perceptual organization. Weinstein and Grether (20) have demonstrated that the minimum visual acuity of *Macaca mulatta* is within normal human limits, and Grether (3) found that color discrimination throughout most of the visible spectrum is similar in the rhesus monkey and man. In a minor study at the Wisconsin laboratory it was observed that normal monkeys and most brain-injured animals could be trained to detect consistently the presence or absence of a $\frac{1}{64}$-sq.-in. circle on a 3 by 3-in. square. Thus, although the area of all stimuli used in this experiment was far above the monkey's limen, differentiation between the small-area stimuli was much more difficult than differentiation between the larger-area stimuli.

Similar discrepancies between the sensory threshold and the perceptual threshold for efficient learned discrimination have been observed in primates and carnivores. Harlow (4) and Warren (17) found that colored patterns are poorly discriminated even when the figures are well above the acuity threshold, and a number of workers have found that highly consistent responses to form per se deteriorate when the size of the figures is reduced to small, but definitely supraliminal, values (1, 11, 16).

Although there is only a low correlation between the sensory and perceptual capacities of monkeys, the results of this study show that perceptual behavior in response to areal and to positional-arrangement differences is intrinsically lawful in this species. These results are also in keeping with the findings obtained in earlier experiments.

Klüver (12) and Gellermann (2) have presented data which indicate that the predominant tendency in pattern discrimination by infrahuman primates is to respond to the object qualities of whole cards rather than to the discernible patterns on the cards. Klüver (12) observed that Java macaques trained on a size discrimination between planometric objects showed zero transfer when required to discriminate the same stimuli on identical backgrounds (i.e., after they had been transformed into patterns). Harlow (5) obtained similar results in an analogous situation. Gellermann (2) trained chimpanzees and two-year-old children to choose a triangle versus a square. When tested with a small square on a large-triangle background versus a small triangle on a large-square background, the children responded positively to the small triangle, but the chimpanzee chose the large triangular stimulus.

These studies indicate that in pattern discriminations such as those of the present investigation, the monkey responds more strongly to the borders than the centers of the cards. Performance should, therefore, be facilitated if the differentially colored areas are large relative to the area of the background, and if the colored cue is in close proximity to the border of the card. This hypothesis is in obviously good agreement with the ranking of the stimulus categories by area and by positional arrangement.

Additional corroboratory data were obtained in two minor studies by the author (18). He found that the relative area of the colored differentia was a significant determinant of the accuracy of patterned color discriminations, but over a wide range of values absolute area was not a highly influential determinant. It was also observed that small colored squares of equal area differed significantly in discriminability with variations in the locus of the colored cue from the center to the borders of the background square, with the peripheral loci being most discriminable.

Harlow (4), in his studies of discrimination learning, demonstrated striking differences between the ability of monkeys to discriminate stimuli that differed in multiple dimensions or *total* surface colors and the stimuli which had surfaces that were in part identical (e.g., two differentially colored patches centered on identical backgrounds). On the basis of these very striking differences he classified such problems as "object discriminations" and "patterned discriminations." The data of the present experiment strongly indicate that these classifications do not represent a true dichotomy, for two stimuli that differ in total surface colors are no more readily discriminated than stimuli in which 75 per cent (or presumably more) of the total surface areas differ. Thus, "patterned discriminations" and "object discriminations" represent merely different positions on a particular stimulus continuum, and not truly differential categories.

SUMMARY

Eight rhesus monkeys were tested on a series of 450 patterned color discriminations. The stimuli varied in the area and the positional arrangement of the differentially colored figures. Significant differences in the percentage of correct responses, and different rates and asymptotes of intraproblem learning, were obtained as a function of these variables. The data could not be explained in terms of any peculiarities of the monkey's sensory capacities. A discussion of the characteristics which differentiate perceptual organization in the higher infrahuman primates from the type of organization found in man leads to the conclusion that functions relating performance to area and positional arrangement might be explained by two factors, the area of the figure relative to the ground and the proximity of the colored patterns to the border of the card.

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EFFECT OF GEOMETRICAL REGULARITY ON VISUAL FORM DISCRIMINATION BY MONKEYS[1]

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This experiment was designed to determine the effect of variation in two stimulus dimensions upon the learning of patterned form discriminations by monkeys, the dimensions being (*a*) the geometrical regularity-irregularity of the figures and (*b*) the absolute areas of the figures.

Gestalt theory states that simple figures, such as circles and squares, are immediately perceived as distinctive wholes, e.g., Köhler writes, "Simple and regular wholes, also closed areas, are formed more readily and more generally than irregular and open wholes" (9, p. 145). The theory implies that the "good" Gestalten of regular figures should be more easily differentiated from one another than the "poor" Gestalten of irregular figures. The same prediction can be deduced from premises other than the innate factors of the Configurationists. Hebb (6) discussed the differences in the associability of stimulus patterns with differential responses and described regular figures and Thorndike figures (12) as representatives of opposite extremes. The identifiability of a figure, of which associability is one aspect, is determined by the degree to which it approaches geometrical regularity. According to Hebb, straight lines and angles dominate in pattern perception. He holds that "the figure made up of straight lines, instead of irregular curves, has special physiological properties" (6, p. 82) which determine maximally discriminable patterns of eye movements and, therefore, readily learned identifiability.

The experimental data on this problem are limited. Lashley (10) observed that rats learned to discriminate highly irregular "Thorndike figures lacking identifiability" as readily as regular geometrical forms.

Harlow (4) found discriminations between small (½-in.) patterns were learned more slowly than problems involving large (2-in.) patterns. The influence of the absolute area of the differential stimuli on the generalization of overlearned geometrical "concepts" has also been investigated by Gellermann (2, 3) for the child and chimpanzee, Klüver (8) and Neet (11) for the monkey, Karn and Munn (7) for the dog, and Fields (1) for the rat.

The methodology of the present experiment is similar to that employed by Lashley and by Harlow, in that the joint effects of regularity-irregularity and of variations in figure area are measured by error scores on a number of independent learning problems. A deliberate attempt has been made to avoid the complications arising from the interproblem transfer which is developed in concept-formation experiments.

METHOD

Subjects

Seven adolescent rhesus monkeys (animals No. 156, 157, 158, 159, 161, 162, and 164) served as *S*s in this experiment. The group's previous laboratory learning experience consisted of 57 days' testing on planometric and stereometric object discriminations (5) and 45 days' training on patterned color-discrimination problems (12).

Apparatus

The Wisconsin General Test Apparatus was utilized throughout this experiment. The 60 patterned stimuli were made by mounting figures cut from black construction paper upon 3 × 3-in. squares of white posterboard. The ten forms used are illustrated in Figure 1. Five figures are geometrically regular, i.e., their contours may be described by algebraically simple equations, whereas the other figures are irregular and complex and would be difficult to describe mathematically or verbally. All ten figures appeared in six sizes: 0.9, 1.8, 2.7, 3.6, 4.5, and 5.4 sq. in., and these areas were equivalent to 10, 20, 30, 40, 50, and 60 per cent of the background card.

The equation of the areas of the irregular figures to those of the regular forms was accomplished by use of a chemical balance. The weights, and presumably the areas, of the regular and irregular forms were equated for each of the six sizes. Progressively larger irregular figures were made by successive tracings of models. Unfortunately, the maximum linear dimensions of some of the irregular figures at areas 4.5 and 5.4 sq. in. slightly exceeded 3 in., and some distortion was introduced by the small modifications necessary to fit these figures onto the background card.

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[1] This experiment is part of a dissertation conducted under the direction of Professor Harry F. Harlow and submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology at the University of Wisconsin in 1953.

[2] Now stationed at the United States Air Force School of Aviation Medicine Primate Laboratory, University of Texas, Austin, Texas.

The ten figures taken two at a time yielded 45 paired comparisons, of which 10 were between two regular forms (R-R), 10 between two irregular forms (I-I), and 25 between one regular and one irregular form (R-I). These paired comparisons between figures were orthogonal to the six areas, so that a total of 270 different stimulus pairs was formed.

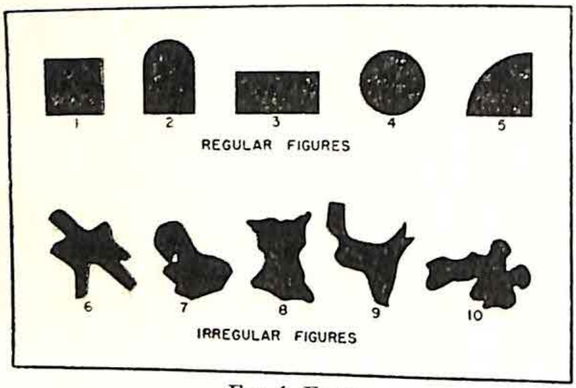

FIG. 1. Forms

Procedure

The individual test-trial procedure was the same as that described in the previous experiment (13). Each discrimination problem consisted of 15 trials with the stimuli differing only in the form of the figures upon them. Six different problems, one at each value of the area variable, were tested each day for 90 days. Since area and paired comparisons were orthogonal, the 90 days' testing permitted two complete replications of the 270 combinations and permitted an unequivocal test of the significance of learning.

Comparisons involving the same two forms are never tested on the same day, and the (+) and (−) forms are randomly altered from pair to pair to minimize interproblem transfer. To prevent the use of secondary cues, fresh cards were frequently substituted for those which had become soiled by the *E*s' or *S*s' handling.

Experimental Design

A factorial design was used, in which the variables of area, *S*s, replications, and types of paired comparisons (R-I, I-I, R-R) were orthogonal. The number of problems within the three classifications of comparisons was unequal, the R-I problems being two and a half times as frequent as either the I-I or R-R discriminations. The alternative of selecting an arbitrary sample from the R-I comparisons was rejected since it was assumed that the advantages of exhausting the limited population of problems outweighed the difficulty of equating the number of problems within categories (which might involve under- or overestimation of the relative difficulty of the regular-irregular discriminations).

RESULTS

Performance, as measured by percentage correct trial 2 to 15 responses, is plotted as a function of the area of the figure, with the type of comparison as a parameter, in Figure 2. Discrimination performance on the R-I problems was superior to that on I-I or R-R at all points, and the only large differences between I-I and R-R appear in favor of R-R at areas 4.5 and 5.4 sq. in. There was a clear increment in performance on the three categories with increases in area, except for the last two points on the I-I curve.

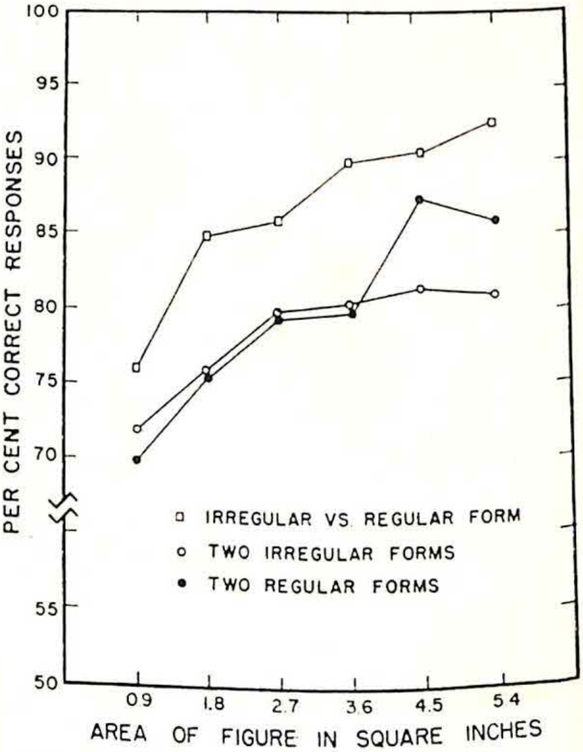

FIG. 2. Performance as a function of figure area

The analysis of variance is summarized in Table 1, with the *F* ratios for the main effects being tested against the largest appropriate interaction. Variation in performance resulting from both area and the types of comparison is significant at the .1 per cent level of confidence. The difference between problem blocks (i.e., practice) is not statistically significant.

Significantly fewer errors as measured by *t* tests of related measures were made on the R-I problems than on the I-I ($p < .01$) or R-R categories ($p < .05$). The difference between total errors on I-I and R-R was not significant, nor were these two categories significantly different at the two points of greatest divergence between their curves, i.e., at 4.5 and 5.4 sq. in.

TABLE 1
Main Effects Tested over Largest Significant Interactions

SOURCES	*df*	MS	*F*
Monkeys	6	2203.96	2.49
M × PB	6	884.96	
Problem Blocks	1	469.67	1
M × PB	6	884.96	1.81
Area	5	2375.28	19.05‡
A × PB	5	124.69	
Categories	2	3010.62	25.69‡
M × C	12	117.21	

‡ *F* significant at .001 CL

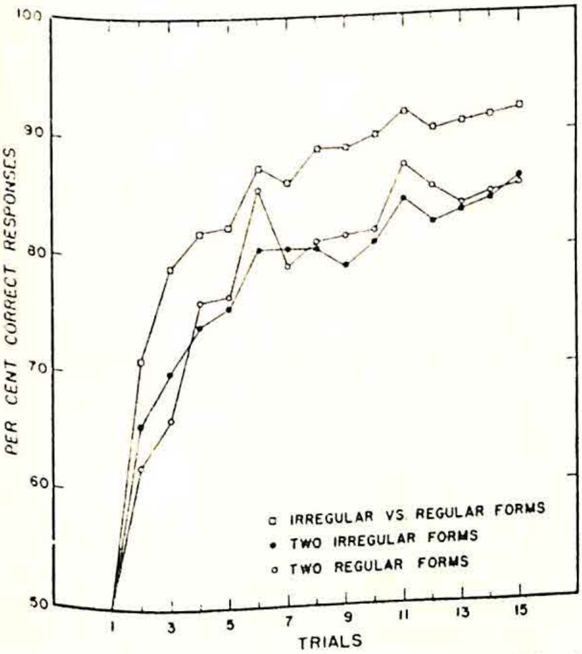

FIG. 3. Intraproblem learning on the three kinds of comparisons

Intraproblem learning on the three kinds of comparisons is shown in Figure 3. This function again shows that performance on the R-I category is superior to either I-I or R-R, and that the latter two do not differ consistently. Observation suggests that the R-I curve differs in slope and asymptote from the I-I and R-I curves, and these latter two might be fitted by the same logarithmic growth function.

The same intraproblem learning data are plotted as a function of the area of the figure in Figure 4. There are irregularities along each of the individual curves, and some overlapping between curves occurs, but it is apparent that as the area of the figure is increased, there is a continuous increase in the rate and final level of intraproblem learning.

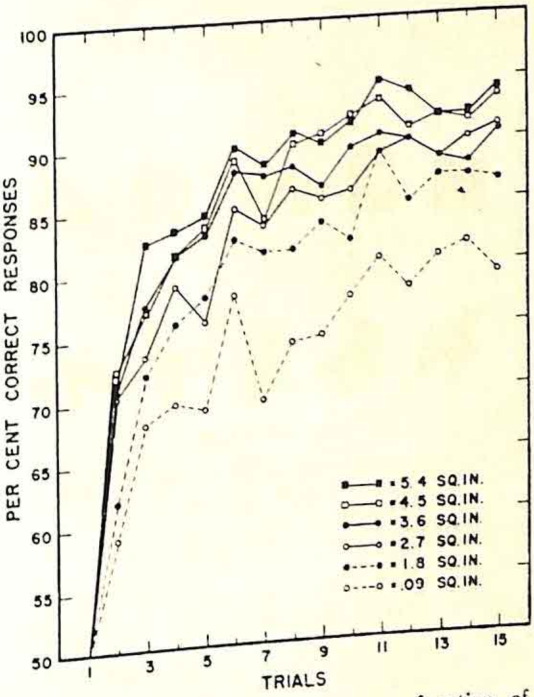

FIG. 4. Intraproblem learning as a function of figure area

DISCUSSION

The results of this experiment show that the discrimination of patterned forms is significantly affected both by the nature of the figures compared and by their area. No significant improvement in performance was demonstrated in the 90 days of testing.

These data obviously do not verify either the implications of Hebb's theory or those of *Gestalttheorie*. Neither system indicates that regular and irregular figures should be equally discriminable. The failure to observe significant learning in three months of testing is not in accord with Hebb's theory of learning to perceive, for one might expect consistent improvement and high level of efficient performance if Hebb's theory were a valid basis for the prediction of behavior in this situation.

The results of this study disagree with Harlow's (4) observation that the difference between large and small figures becomes insignificant with practice. Harlow's animals were experimentally naive, and it may be supposed that such animals would show some improvement in discrimination learning; *S*s tested in this study had 102 days of testing before being tested on patterned form discriminations and may very well have reached the limit of learning-set formation, so that differences in performance determined by stimulus parameters would be permanent and irreducible.

The results of this experiment are in good agreement with those of the previous experiment in indicating that increases in the area of supraliminal figures improve the discrimination of patterns, and add a further indication of the monkey's perceptual organization—regularity and irregularity form two dimensions of similarity in the monkey, as in man, inasmuch as discrimination within these continua are inferior to discriminations between them.

SUMMARY

A group of seven normal macaques was tested on a series of 540 patterned form-discrimination problems. Two hundred and seventy pairs of stimuli varying in area and geometrical regularity were replicated so that the effect of learning could be evaluated. The results showed that discriminability was an increasing function of the area of the figure, and that monkeys made significantly fewer errors in discriminating between a regular form and an irregular form than in discriminating two regular or two irregular forms.

Discrimination of two irregular forms was not significantly inferior to differentiation of two regular geometrical forms. No improvement in performance was noted in 90 days of testing. These results disagree with the implications of the theories of Hebb and Gestalt psychologists.

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INFLUENCE OF SIMILARITY OF CHOICE-POINT AND GOAL CUES ON DISCRIMINATION LEARNING

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Several studies of discrimination learning (1, 3, 6, 7) have indicated that when the positive and negative goal boxes are identical, or highly similar, the rate of learning is slower than when these boxes are discriminably different. The usual interpretation of this result has been in terms of the generalization of secondary reinforcement between them. Further, it is assumed that if there is generalization of secondary reinforcement from the positive goal box to the positive choice-point cue, learning will be more rapid than in the absence of such generalization. Conversely, if secondary reinforcement generalizes to the negative choice-point cue, learning will be slower than in the absence of such generalization.

The above assumptions are usually formulated in terms of secondary reinforcement, but because of the symmetry of the situation it is necessary to postulate similar types of generalization between goal boxes and between the negative goal box and the choice-point cues in terms of conditioned inhibition. This should retard learning when it generalizes to the positive goal box or to the positive choice-point cue, and facilitate learning when it generalizes to the negative choice-point cue.

The present experiment is designed to test the adequacy of some of the implications of this formulation in a black-white brightness discrimination, and to measure the relative influences of these various types of generalization effects. Assuming a constant delay interval between the choice-point cues and the goal boxes, there are essentially three variables that control these various types of generalization: (*a*) the similarity of the two goal boxes, (*b*) the similarity of the positive goal box and the positive choice-point cue, and (*c*) the similarity of the negative goal box and the positive choice-point cue. If these are specified, then the similarity of each goal box and the negative choice-point cue is determined. The extremes of these various degrees of similarity can be checked by taking all possible combinations in which the positive choice-point cue is either black or white, the positive goal box is either black or white, and the negative goal box is either black or white. This factorial design calls for eight groups of animals. But to complete it, a control group is essential for which there is complete generalization between goal boxes and between each goal box and the choice-point cues. The animals in this control group presumably would have to learn the discrimination on the basis of trace processes without any differential effect from either secondary reinforcement or conditioned inhibition. Thus, they would form a base line against which to compare the rate of learning in the other groups. This control can be achieved by having black-white choice-point cues and black-white goal boxes, but with a random pairing of goal boxes and choice-point cues on successive trials. This should result in complete generalization of secondary reinforcement and conditioned inhibition between goal boxes and between each goal box and each choice-point cue. This design is outlined in Table 1.

According to the theoretical analysis outlined above, Group I should learn most rapidly because all generalization factors are operating in its favor; there is no generalization between goal boxes, the secondary reinforcement generalizes to the positive choice-point cue, and the conditioned inhibition generalizes to the negative choice-point cue. Group II should learn most slowly, if at all; there is no generalization between goal boxes, but all the secondary reinforcement generalizes to the negative choice-point cue and all the conditioned inhibition to the positive choice-point cue. The order of the other three groups should depend upon the assumptions made about the relative amounts of generalization of secondary reinforcement and conditioned inhibition. If only secondary reinforcement generalizes or generalizes more strongly than conditioned inhibition, then Group III should learn most rapidly and Group IV most slowly, if at all, of these three groups. Conversely, if only conditioned inhibition generalizes or generalizes more strongly than secondary reinforcement, the opposite order of the three groups would be expected. If both secondary reinforcement and conditioned inhibition tend to generalize to the same extent, little or no differentiation between groups would be expected. Thus, the rate at which these groups learn this brightness discrimination should be a rough index of the adequacy of the theory and of the relative influences of these various types of generalization. The failure to obtain these predicted orders would indicate that the concepts of secondary reinforcement, conditioned inhibition, and their generalization are inadequate as they now stand to account for the results.

TABLE 1
Experimental Design

GROUP	POSITIVE CUE	POSITIVE GOAL BOX	NEGATIVE GOAL BOX
I *a*	B	B	W
b	W	W	B
II *a*	B	W	B
b	W	B	W
III *a*	B	B	B
b	W	W	W
IV *a*	B	W	W
b	W	B	B
V*a*	B	Randomly B or W	Randomly W or B
b	W		

METHOD

The *S*s consisted of 50 albino rats, 23 males and 27 females, ranging from 100 to 150 days of age at the beginning of the experiment.

The simultaneous discrimination apparatus was modeled after one employed by Grice (3). It consisted of a starting box which opened, by means of a 2-in.-wide alley, into a V-shaped choice chamber. All these compartments were painted a mid-gray. Extending from the choice chamber were two parallel alleys, 4 in. wide and 4 in. deep. Each alley consisted of three sections. The first part of each alley was the stimulus section (15 in. long), the second a neutral gray section (18 in. long), and the third a goal box (15 in. long). The stimuli consisted of two brightnesses obtained by painting one stimulus section white and the other black. These sections could be interchanged on successive trials. The goal boxes on any given trial were either both white, both black, or one white and one black, depending upon the group of animals being run. They could be interchanged on successive trials. Two inches from the entrance of each section in each alley there was a curtain the same color as that section. In addition, a gray curtain was hung 2 in. from the end of each gray section, so as to prevent *S*'s seeing the color of the goal box until it had reached it. Vertical sliding doors were located at the entrance to each stimulus section and at the beginning and end of the gray sections. The apparatus was covered with ½-in. wire mesh and illuminated by a 500-w. lamp 7 ft. above the stimulus sections.

The animals were tamed and then habituated to a 24-hr. feeding cycle by giving them 8 gm. of Purina Dog Chow at the same time each day for seven days. The following two days they were trained to eat small pieces of wet mash in a gray goal compartment, which was used only in this preliminary training. This adaptation training was continued until each animal would readily push under a gray curtain and immediately eat the available food. On each of the following two days, all animals were given 10 forced trials in the apparatus, with right-left and black-white choices balanced. Gray goal boxes were used. Each trial was rewarded.

Following the preliminary training, the animals were divided randomly into ten groups of five *S*s each, containing approximately equal numbers of males and females. All groups were trained on the black-white discrimination by exactly the same procedure. The groups differed only in the relationships that existed between the brightnesses of the goal boxes and the brightnesses of the positive and negative stimuli at the choice point. These different relationships for the ten groups are indicated in Table 1.

All animals were given 10 trials per day at approximately 10-min. intervals. A correction method was used. When an animal made the wrong choice, it was immediately taken out of the goal box and run again until the correct choice was made. Thus, a trial consisted of one correct choice. The position of the positive cue on successive trials was RLRRLLRLLR. For Group V, the goal-box and choice-point brightnesses corresponded on trials 2, 3, 5, 8, and 10, i.e., both were black or both were white. They were of opposite brightnesses on the remaining trials, i.e., one was black and the other white. As a control, new stimulus compartments were introduced during training. All animals were trained to a criterion of 18 correct choices in 20 consecutive trials. Each animal was then given 40 additional trials to check on the reliability of the criterion and to ensure overlearning. At the end of the day's run, each animal was given sufficient additional food to bring the total up to 8 gm.

Upon completion of this original learning, all animals were trained on the reversed discrimination, i.e., the initially positive cue was made negative, and conversely. It should be noted that this procedure results in an interchange of the relationships between the goal and choice-point cues for Groups III and IV but not for the other groups. During this reversal training, a noncorrection method was used so that each trial consisted of one, and only one, choice. Otherwise the apparatus and procedure were unchanged. The criterion was again 18 correct out of 20 consecutive choices, with

40 additional postcriterion trials. If an animal had not reached this in 200 trials, it was returned to the correction procedure.

RESULTS

The results of this experiment are presented in two parts: (*a*) the data on original learning by the correction method, and (*b*) the data on the reversal learning by the noncorrection method.

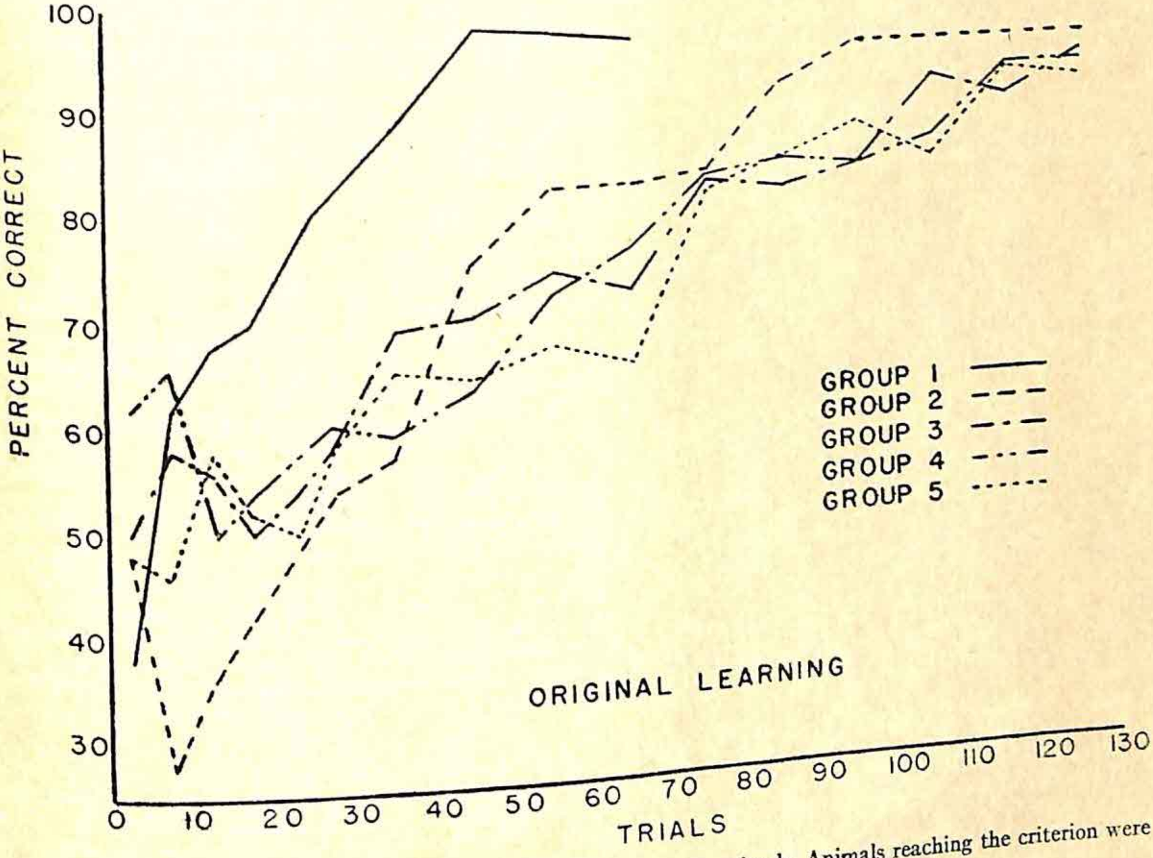

Fig. 1. All points beyond trial 100 are based on fewer than ten animals. Animals reaching the criterion were assumed to have continued at the 95 per cent level of accuracy.

Original Learning

The learning curves for the five groups are presented in Figure 1. Group I shows the relatively rapid learning to be expected from this type of pairing of choice point and goal boxes. Group II, on the other hand, shows an initial piling-up of errors as though learning the converse discrimination, but from trial 20 on, tends to learn at about the same rate as Group I. The other three groups are indistinguishable and show a gradual improvement that is slower than that of either of the other two groups.

The group means for trials to the criterion are given in Table 2.

The statistical significance of these differences was determined by assigning each animal a score that was the square root of the number of trials it required to reach the criterion of 18 out of 20 correct initial choices, thus equating the variances within groups. The resulting analysis of variance involved two variables, the differences between the five major groups and the differences between those animals having black as the positive choice-point cue and those having white as the positive choice-point cue. In this analysis both the differences between groups and the interaction term were significant at the .01 level of significance. Then t tests between pairs of group means were computed using the error term of the analysis of variance. This analysis indicated that Group I learned significantly more rapidly than any other group (.01 level), that Group II learned significantly more rapidly than the remaining three groups (.05 level), and that these latter were indistinguishable.

A similar analysis was made of the total runs required by each animal to reach the criterion. These means also are shown in Table 2. In the correction method more than one run per trial is possible. Group I was again significantly better than any other group (.01 level), but Group II, even though its mean was slightly less than the means of the other three groups, was not significantly better than the rest. This discrepancy between the analysis of total runs and total trials (as herein defined) indicates that in terms of number of reinforcements required, Group II was significantly better than the remaining three groups, but that this group tended to make more repetitive errors on a given trial than did the other groups, thus canceling out any distinction between them in terms of total runs.

TABLE 2

Means at Various Stages of Learning

GROUP	ORIG. LEARNING		OVER-LEARNING ERROR TRIALS	REVERSAL TRIALS	
	Trials	Runs		Ex-tinction	Re-learning
I *a*	14.6	26.8	0.8	41.4	14.4
b	30.0	47.6	1.6	38.4	32.4
aver.	22.3	37.2	1.2	39.9	23.4
II *a*	56.2	115.6	2.2	84.8	24.2
b	37.2	92.2	3.4	83.2	16.4
aver.	46.7	103.9	2.8	84.0	20.3
III*a*	53.2	97.2	3.8	76.8	68.8
b	81.8	143.4	4.0	89.8	49.8
aver.	67.5	120.3	3.9	83.3	59.3
IV *a*	82.0	135.2	4.2	72.6	139.0
b	65.6	119.0	3.2	64.6	108.2
aver.	73.8	127.1	3.7	68.6	123.6
V *a*	58.2	99.4	4.0	118.2	141.0
b	90.2	158.8	3.2	103.0	62.2
aver.	74.2	129.1	3.6	110.6	101.6

This tendency toward repetitive errors by Group II occurred most strongly in the first 20 trials. Thereafter the reduction in repetitive errors of this group was as rapid as of Group I. During the first 20 trials, Group II animals appeared to be learning the opposite discrimination from the one assigned them. This impression was confirmed by computing the mean number of error trials for this group during these 20 trials and, by means of a t test, comparing it with chance expectancy. The result was a t value significant at the .01 level, indicating that more than a chance number of initial error choices were made during this period. Once this tendency to make the wrong discrimination was extinguished, however, the rate of learning in this group was not too different from that of Group I.

All groups in this experiment were run for 40 trials beyond the criterion to determine the level of accuracy they could maintain. The mean error trials during these runs are shown in Table 2. An analysis of variance and t tests similar to the previous ones were computed for these data. All groups maintained better than a 90 per cent level of accuracy, but Group I was significantly better than Groups III, IV, and V (.01 level), these latter being indistinguishable. Group II was midway between Group I and the others but not significantly different from either. Thus, Group II not only tended to learn slightly more rapidly than Groups III, IV, and V, but also tended to maintain a higher level of accuracy on this discrimination during overlearning.

TABLE 3

Analyses of Variances

FACTORS	*df*	ORIGINAL TRIALS	LEARNING RUNS	RE-VERSAL EX-TINCTION
Preference				
+C.P (B vs. W)	1	0.50	1.45	.001
+G.B (B vs. W)	1	22.82†	23.06*	.003
−G.B (B vs. W)	1	0.01	0.12	.003
Generalization				
+C.P+G.B (S vs. D)	1	14.56†	46.27†	.456†
+C.P−G.B (S vs. D)	1	8.33*	38.05†	.141*
+G.B−G.B (S vs. D)	1	65.36†	80.34†	.102
Triple Interaction	1	0.05	0.14	.006
Error	32	1.99	3.37	.028

Note.—These analyses are based on transformed scores in order to achieve homogeneity of variance. Square roots of the indicated values were used on the original learning data, logarithms on the reversal data. The relearning data for the reversed discrimination are not included because of the change in procedure from noncorrection to correction training after the two hundredth trial.

* Significant at the .05 confidence level.

† Significant at the .01 confidence level.

Additional insight into the factors controlling the rate of learning in this situation results from a factorial analysis of the number of trials each animal required to reach the criterion. If only Groups I through IV are considered, the experimental design involves three experimental variables, each of which occurs in two degrees, as indicated previously. This factorial analysis, first for trials to the criterion and then for the total runs to the criterion, is given in Table 3. In each instance the only preference factor that proved to be statistically significant was the influence of black in contrast to white at the positive goal box. Neither the specific brightness of the negative goal box nor the positive choice-point cue had measurable influence on the rate of learning. In both analyses, all three generalization factors (first-order interactions) were significant, the similarity between goal boxes tending to be somewhat more important than the other two in each case. The main difference between the two analyses was in the greater relative weight given to the generalization between negative goal box and positive choice-point cue when total runs were considered, as would be expected from the inclusion of repetitive errors in the latter measure. This analysis of total runs tended to give equal relative weight to the amount of generalization from either goal box to the choice-point cues.

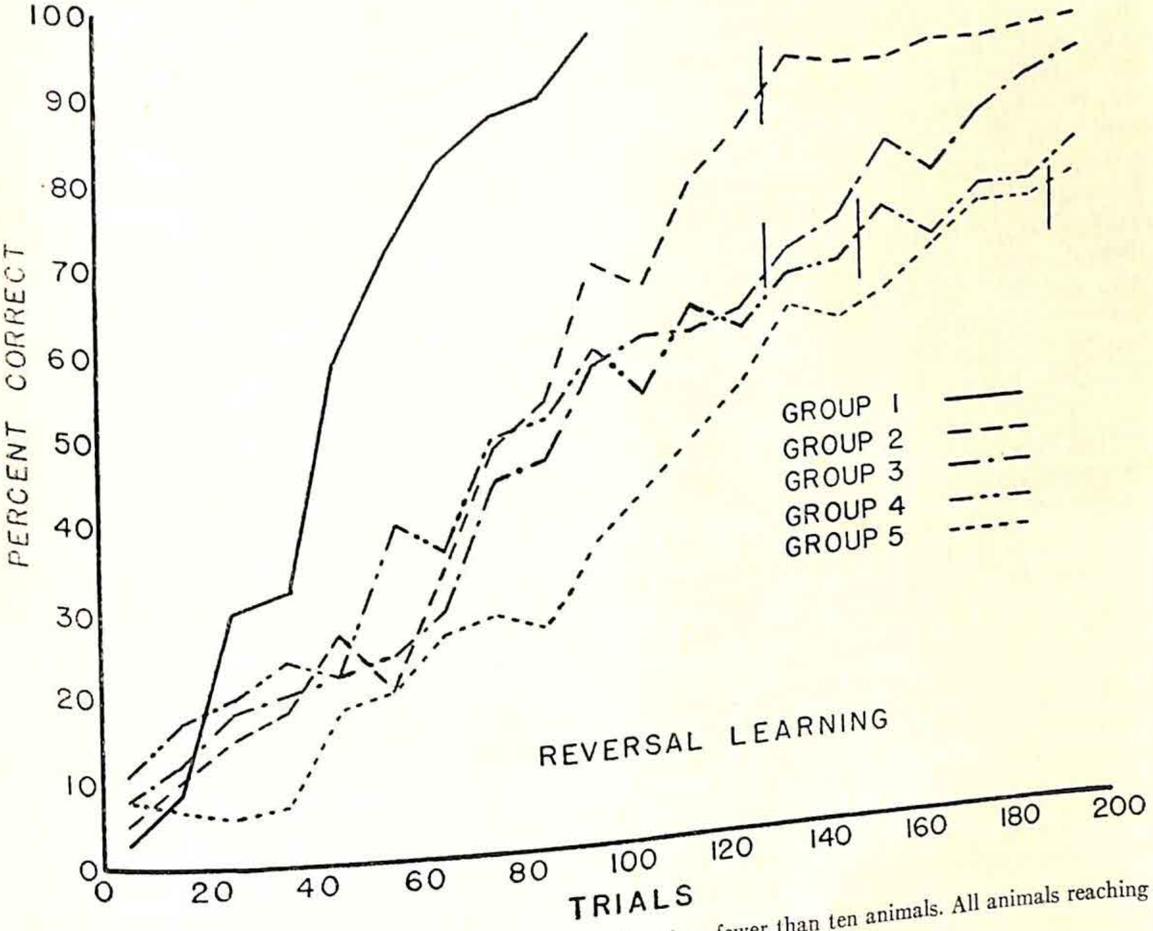

FIG. 2. All points to the right of the vertical lines are based on fewer than ten animals. All animals reaching the criterion were assumed to have continued at 95 per cent accuracy.

Reversal Learning

After each animal had reached the criterion of original learning and had an additional 40 trials of training, it was given the reversed brightness discrimination using a noncorrection method for 200 trials. The learning curves for the reversal discrimination are shown in Figure 2.

Groups I and II again learned most rapidly whereas Group V appeared to learn most slowly. All animals in Groups I and II reached the criterion during the first 200 noncorrection trials, nine animals in Group III did so, whereas only five animals in Groups IV and V reached this level. Because of the change in training procedure at trial 200 (use of a correction in place of the noncorrection method), a statistical comparison of these differences cannot be based on an analysis of variance of trials to criterion. However, pairs of groups can be contrasted by using Festinger's rank-order test (2). This test indicated that Group I was significantly better than each of the other groups (.01 level), that Group II was significantly better than Groups IV and V (.01 level) and somewhat better than Group III (.05 level, approximately). The only other significant difference indicated that Group III was superior to Group V (.05 level).

A more meaningful analysis of these data results if the total runs to the criterion for each animal are divided into two parts: (*a*) trials required to "extinguish" the original discrimination, and (*b*) trials required to learn the reversed discrimination. Consequently, for each animal the 20 consecutive trials during which it first made 10 or more correct responses to the reversed discrimination was determined. The mid-point of this interval was taken as the 50 per cent or chance level of preference for the two choice-point cues. The number of trials to this point were considered to be "extinction" trials of the original discrimination. All runs beyond this, whether by the correction or noncorrection method of training, were considered to be learning trials on the reversed discrimination.

The mean number of "extinction" trials for each group is shown in Table 2. The order of groups in terms of rapidity of extinction was I, IV, III, II, and V. Group I extinguished significantly faster (.01 level) than any of the other groups and Group IV significantly faster than Group V (.01 level). The other differences are not significant. A factorial analysis of the scores for the first four groups, shown in Table 3, indicated that only the similarity between the new positive goal box and the new positive choice-point cue, and possibly the similarity of the new negative goal box and the positive choice-point cue, had any significant influence on the rate of extinction. Similarity between the goal boxes or preferences for a given brightness was not of differential influence.

The mean number of runs required by each group to go from the 50 per cent point to the criterion of learning on the reversed discrimination also is shown in Table 2. The means for Groups IV and V are considerably underestimated. Five animals in each of these groups had to be returned to the correction procedure before reaching the criterion, and this is probably a more efficient method of training than the noncorrection method used on the other groups. Despite this underestimation, Groups I and II, while not significantly different, were each better than any of the other groups (.01 level). Group III was not significantly better than either IV or V ($p < .10$). The main differences between these results and similar ones for the original learning were (*a*) the obvious equality of Groups I and II, (*b*) the fact that Group III, which now had both goal boxes similar to the negative choice-point cue, was somewhat better, though not significantly, than either IV or V, and (*c*) Group IV, which now had both goal boxes similar to the positive choice-point cue, was slightly though not significantly poorer than the control group. In the original learning these three groups were indistinguishable. These differences on the reversal learning were primarily a function of the strength of the tendency to revert to position habits; Groups I and II showed little if any such tendency, but it was very marked in Groups IV and V and of an intermediate degree in Group III.

DISCUSSION

The results for original learning indicate that Group I (normal group) learns this discrimination at a rate comparable to that obtained previously by Grice (3) even though the training method is somewhat different. In the case of Group I the rapid learning and reversal can be accounted for by the lack of generalization between goal boxes and maximal generalization between each goal box and the appropriate choice-point cue. In the case of Group V, it must be assumed that the original learning was largely in terms of a visual-trace process, as generalization was symmetrical between goal boxes and between each goal box and the two choice-point cues. The slowness of "extinction" in this group emphasizes that such traces only gradually build up conditioned inhibition as well as positive habit strength.

The similarity in performance of Groups III and IV to that of Group V during original learning suggests that secondary reinforcement and conditioned inhibition, if these concepts are to be used to explain the results, must be of equal importance in the control of behavior in this situation. If secondary reinforcement were the only factor involved, or were much more influential than conditioned inhibition, the order of groups should have been III, V, IV. The converse order should have resulted if conditioned inhibition were the dominant factor. The equality of the three groups indicates that either they were of equal influence or that some other concepts must be employed to explain the results.

This interpretation is complicated by the results on the reversal learning. Group III, which now has both end boxes similar to the negative choice-point cue, relearns the reversed discrimination more rapidly (but not significantly) than did either Group IV or V. Group IV, which now has both goal boxes the same as the positive choice-point cue, tends to be slower than Group V, though the difference does not reach significance. These data for reversal suggest that conditioned inhibition and its generalization is more determinative of performance than secondary reinforcement and its generalization. This difference in results between original learning and reversal may result either from the change from a correction to a noncorrection procedure, or from the transfer of some unidentified but differential habit or tendency from the original discrimination to the reversal.

These interpretations are supported by the results of the factorial analysis. During original learning, there were three significant factors controlling the rate of learning: (*a*) similarity between goal boxes such that when they were identical, learning was slower than when they were differentiated, (*b*) similarity between the positive goal box and positive choice-point cue, such that when they were identical, learning was faster than when they were differentiated, and (*c*) similarity between the negative goal box and the positive choice-point cue, such that when they were differentiated, learning was faster than when they were identical. Only the first factor differentiated the groups during the 40 trials of overlearning, and only the latter two reached significance during "extinction."

The one additional factor of interest in these analyses is the lack of any brightness preference except for the positive goal box. In each of the four major Groups I to IV, that subgroup having a black positive goal box learned more rapidly on the original discrimination than did its corresponding subgroup having a white goal box, irrespective of the brightness of the choice-point or negative goal-box cue. During extinction of the original discrimination and the learning of the reversed discrimination, this factor no longer gave differential results. The implication is seemingly that a preference of this sort is activated primarily in the presence of positive reinforcement. The failure of the brightness preference to manifest itself at the choice point or in the negative goal box indicates that it does not operate automatically but only when activated by the reward. The fact that it is no longer operating to a measurable degree during the 40 overlearning trials or during extinction and reversal suggests that its influence is in the early stages of learning, after which it is equalized.

The most intriguing result of this experiment is the performance of Group II, the one having a reversed relationship between the goal-box and choice-point brightnesses. Initially, these animals tended to learn the wrong discrimination, as would be expected in terms of the concepts discussed above, but after the first 20 trials this tendency disappeared. They then learned the correct discrimination at about the same rate as the Group I animals. Similarly, when trained on the reversed discrimination by the noncorrection method, they learn this as rapidly as Group I animals (once extinction of the original discrimination was complete) and significantly more rapidly than the other groups.

One obvious explanation of this behavior is that during the initial trials these animals established a discrimination between the choice-point cues and the goal-box brightnesses. Once this discrimination was established, then generalization between goal boxes and choice-point cues disappeared. Consequently, later learning was not confused by this factor as it was in Groups III, IV, and V. But in granting that such a discrimination was established, two additional problems are raised. First of all, it is not clear, at least to the present authors, that a discrimination of this sort fits the usual paradigm of learning, i.e., in what sense positive or negative habits to these two sets of cues can be established or maintained under these training conditions. Secondly, and more importantly, even if such a discrimination existed, it is not apparent why Group II should have learned about as rapidly as Group I when all the generalization factors presumably favored rapid learning in the latter group and were excluded by the discrimination in the former. Rather, it would be anticipated that Group II would have to learn largely on the basis of visual trace processes and, therefore, would be no more rapid than Group V.

One possible explanation of this second problem is in terms of the "acquired distinctiveness of cues" (4, 5). During the first 20 trials the Group II animals did learn a black-white discrimination at the goal boxes which transferred to the choice point, as exemplified by the significant number of errors made in the early trials. In part because of the correction procedure used, these animals seemingly built up strong "emotional" reactions to the negative goal box as indicated by biting, refusal to enter for long periods, etc., whenever they made an error. This was not true of Groups III, IV, and V. Consequently, it is possible that after the establishment of the discrimination between choice-point cues and goal boxes, this tendency to react specifically and strongly to the black-white dimension at the choice point, as the dominant cue in the situation, remained. If so, any trace process based on brightness which was aroused in these animals would be much more "distinctive" than comparable traces in any of the other animals. This would facilitate learning.

SUMMARY

A factorial-design experiment was devised to test the relative influences on the rate of discrimination learning of the generalization of secondary reinforcement and of conditioned inhibition between goal boxes and from goal boxes to choice-point cues. This was accomplished by taking all possible combinations in which the positive choice-point cue was either black or white, the positive goal box was either black or white, and the negative goal box was either black or white. A control group in which there was complete generalization between goal boxes and between each goal box and choice-point cue was obtained by having the positive goal box half the time white, half the time black, and similarly for the negative goal box. Fifty animals, five to a group, first learned this problem and then the reversed discrimination.

During the original learning it appeared that the generalization of secondary reinforcement and of conditioned inhibition were equally effective in determining the rate of learning. But on the reversed discrimination the role of conditioned inhibition proved to be the more influential of the two. The interpretation of this result is complicated by the previous experience of the various groups.

The rapid learning, both initially and during reversal, of the animals having black as a positive cue, but a white positive goal box, and white as a negative cue, but a black negative goal box, raises problems for the usual interpretation of discrimination learning. One possible explanation is in terms of a discrimination set up between choice-point cues and goal-box brightnesses which effectively prevented generalization between the two But this must be supplemented by the assumption that the choice-point cues had "acquired distinctiveness" as the result of previous experience.

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DEPRIVATION OF VISUAL FORM DEFINITION IN THE RING DOVE: II. PERCEPTUAL-MOTOR TRANSFER[1]

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Interocular transfer, the influence of previous experience with one eye on current performance of the contralateral eye, is of particular interest to psychologists because of the bearing of this phenomenon upon theories of function of the central nervous system.

In the bird, there is complete decussation at the optic chiasma, so that as far as we know, all the fibers of the optic tract from the right eye have connections with the left tectum, and conversely for the left eye. Thus, there are no known specific neuronal pathways whereby an image on one retina might cause the ipsilateral visual area to be stimulated. Theories such as Hebb's (2) postulate that interocular transfer, in the bird and in animals with similar retino-cerebro connections, is due to perceptual learning before the experiment began, which may have established hypothetical intracerebral "pathways" called "phase sequences." It is postulated that these phase sequences connect the two tecta and are the basis upon which any later visual transfer which is demonstrated may take place. From this it follows that interocular transfer in birds reared without specific experience in visual form definition and thus lacking the hypothetical phase sequences would be inconvenient to explain by this theory. On the other hand, failure to demonstrate transfer under these conditions would tend to confirm theories such as Hebb's theory and to infirm perceptual theories of the "field" variety, such as Lashley's theory. This latter theory postulates that visual transfer may take place by a "wave" mechanism and that previous involvement of the specific cortical substrate is not a necessary prerequisite for transfer of visual training.

Transfer of a brightness discrimination in the chick has been previously demonstrated by Köhler (3), while Bingham (1) found that transfer of a form discrimination in the chick is doubtful. Levine (4) concluded that transfer of an experimentally established form discrimination occurred in the pigeon when the upper temporal retina was stimulated in training and test sessions, but not when the lower hemiretina was stimulated. However, these experiments do not necessarily provide support for the theory of "inbuilt equipotentiality." The *S*s used in all these experiments had previous visual experience in which both eyes performed part or whole of similar or analogous tasks. Thus, as suggested by Hebb (2), the previous visual experience may have established hypothetical phase sequences which may have been the basis for the transfer and equipotentiality shown.

If ring doves, after having been reared through life in such a manner as to prevent all visual form definition (and which therefore lack the hypothetical phase sequences), then demonstrated transfer of training, the demonstration would be crucial both to the "experience" theory and to the theory of "inbuilt equipotentiality." "Experience" theory under these conditions would predict no transfer whatsoever (0 per cent), while the theory of "inbuilt equipotentiality" would predict immediate (100 per cent) transfer. Both theories, as interpreted by the present author, would predict immediate (100 per cent) transfer in normally reared birds trained and tested for transfer of perceptual-motor training.

METHOD

The complete method of rearing, preliminary training, training in the circle-triangle discrimination, testing for visual acuity, and opthalmoscopic examination of

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[1] This paper is based on part of a dissertation submitted to the faculty of the Department of Psychology of New York University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The author wishes to express gratitude to Dr. T. C. Schneirla for methodological and theoretical aid from the initial planning stages to the final reports of these experiments. Gratitude is also expressed to the Department of Animal Behavior of the American Museum of Natural History for the use of its experimental facilities.

[2] Now at the Institute for Research in Human Relations, Philadelphia.

*S*s, as well as the apparatus, has been previously described (5, 6). In brief, the procedure consisted of first rearing the experimental birds from before the opening of their eyes to time of training under conditions which allowed their retinas to be stimulated by brightness differences ("hood rearing"), but which prevented perception of visual form. Preliminary training to jump from a perch of variable height to the horizontal was then given. Then monocular training was given on a circle versus triangle discrimination to a criterion of nine out of ten correct consecutive jumps to the positive stimulus. Immediately before this specific visual training, an opening was made in the hood of the experimental birds so that images of external stimuli would impinge only on one upper hemiretina. As a further control over the retinal area stimulated, the stimuli to be discriminated were placed subrostrally. Hence, when the terms "uncovered eye" or "eye" are used in this paper, it should be kept in mind that images were confined to the upper hemiretina. A modified Lashley-type jumping stand was used as apparatus. When a bird reached the criterion of learning, the test session was begun at once. During the test session, the opening around the eye which served as afferent avenue of experience in training was covered with masking tape, and a window was made for the contralateral eye.[3] The bird was then tested, as before, as to its ability to reach the criterion under the new conditions.

TABLE 1

Experimental Conditions and Direct Comparisons of Training (T_1), Testing (T_2), and Supplementary Testing (T_3) Scores for Each Group

GROUPS	SERIES	EYE (OR EYES) UNCOVERED	M	SIGMA	% TRANSFER T_1–T_2	% TRANSFER T_2–T_3
Hood-reared						
Group A	T_1	Rl*	123.5	14.2		
	T_2	rL	89.6	18.7	30	98
	T_3	Rl	12.0	1.4		
Group B	T_1	rL	127.6	18.5		
	T_2	Rl	99.3	16.5	24	60
	T_3	RL	45.6	9.2		
Group C	T_1	Rl	119.3	34.5		
	T_2	RL	57.1	23.8	56	88
	T_3	Rl	16.0	2.7		
Group D	T_1	Rl	127.1	25.7	93	—
	T_2	Rl	18.2	6.3		
Normally reared						
Group E	T_1	Rl	72.3	13.4	98	—
	T_2	rL	11.0	1.1		
Group F	T_1	Rl	83.1	16.3	99	—
	T_2	RL	11.0	1.4		

* Right eye half-covered; left eye completely covered.

After reaching the criterion in the test session, birds in certain groups were given additional tests which involved either the use of the eye uncovered in the original training, or of both eyes at the same time. This supplementary testing was performed in the same manner and to the same criterion as was the original training.

Three randomly chosen hood-reared birds and three randomly chosen controls were given opthalmoscopic examination and were tested for visual acuity.[4]

Twenty-four hood-reared birds were randomly divided into four experimental groups of six each (Groups A, B, C, D). Twelve normally reared birds were randomly divided into two control groups of six each (Groups E and F). The control birds were treated in exactly the same manner, except for the method of rearing, as were the experimental animals. The eye(s) used during the training, testing, and supplementary testing periods for each group is shown in Table 1.

TABLE 2

Percentage Transfer, *t*'s*, and *p* Level between Groups Tested Using Same Eye but with Differing Pretraining

GROUP	GROUP COMPARISONS (R, L eye used in training)	*t*	*p*	% TRANSFER
A B	Train using R, then L vs. train using L only	3.22	.05	32 (Group A)
B A	Train using L, then R vs. train using R only	2.51	.05	30 (Group B)
C D	Train using R, then both vs. train using R only	4.48	.01	60 (Group C)

* *t*'s calculated using Cochran's method; $df = 5$.

RESULTS

The means and sigmas for each group in each condition are presented in Table 1.

Intragroup comparisons of training scores, test scores, and supplementary test scores were first made. This type of treatment depends upon the correctness of the assumption that the three experimental conditions were essentially of equal difficulty for the birds. The data so calculated are presented in Table 1.

Comparison of the means of the hood-reared groups in the original training indicates no significant differences between them. This suggests that the groups were equal in initial ability. Therefore, an additional test for transfer may be made according to the general paradigm:

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[3] For one group of birds trained through a single eye and tested using both eyes, the opening in front of the eye used during training was, of course, not covered with tape.

[4] Drs. H. L. Teuber, S. Weinstein, and Josephine Semmes kindly performed the opthalmoscopic examination of the birds.

Group X: Train on Z — Train on P
Group Y: — Train on P

Since the groups have been treated alike in all respects, any difference between the scores on P may be attributable to the training on Z. Following this paradigm, transfer from the right eye to the left eye, from the left eye to the right eye, and from the right eye to both eyes was measured. The resulting data are presented in Table 2.

Tables 1 and 2 both indicate incomplete transfer from training to testing sessions for the hood-reared birds. Under identical experimental conditions the normally reared birds showed almost complete transfer. Moreover, complete transfer was not shown to the binocular situation after the hood-reared birds had learned the discrimination using each eye individually.

TABLE 3

p Levels, t's, and Percentage Transfer between Supplementary Testing Sessions for Groups Trained and Tested with Same Eye but Differing Intermediate Training

COMPARISON	t	p	% TRANSFER
Group A vs. Group D	4.39	.01	76
Group C vs. Group D	1.66	.156	27

Test for transfer of training from the test session to the supplementary-test session may be made according to the general paradigm:

Group X: Train on P—Train on Q—Train on P′
Group Y: Train on P—rest—Train on P′

The difference between the two groups on the final test, P′, is a measure of the transfer attributable to the training on Q. The data presented in Table 3 are derived from this method of treatment.

DISCUSSION

In testing for transfer of training, intragroup comparisons were first made (Table 1). In no case did any hood-reared group show as much transfer from the training session to the test session as did the normally reared groups. A 30 per cent transfer was shown by Group A (hood-reared) from the right eye to the left eye, and a 24 per cent transfer from the left eye to the right eye was shown by Group B (hood-reared). Transfer of 56 per cent was obtained in Group C from a training condition with one eye exposed, to a testing condition in which both eyes were exposed. This was the maximum amount of transfer shown for any of the hood-reared groups. Under identical experimental conditions nearly 100 per cent transfer was obtained from the normally reared groups.

Transfer was very incomplete in hood-reared birds first trained using their left eyes and next their right eyes, when both eyes were then used simultaneously.

Table 2, derived from an alternative method of treating the data, is in substantial agreement with the above interpretation.

Perhaps the best test of the transfer from the initial testing condition to the supplementary testing condition is the paradigm from which Table 3 was derived. This treatment allowed an experimental isolation of the factor of transfer attributable to the testing sessions, since the birds of each group reached the same criterion in the initial training. Treatment of the data from the hood-reared birds in accordance with this design indicated a transfer of 76 per cent from the testing condition with the left eye to the supplementary testing condition with the contralateral eye. The transfer shown from the testing condition in which both eyes were used to the supplementary testing condition with just one eye was not statistically significant.

The nearly 100 per cent transfer found here for the normally reared birds could have been predicted from the perceptual theories of Hebb or Lashley. The results of partial transfer found for the hood-reared birds could not have been predicted from either of these theories. The assumption is made here that these theories are intended to hold at this phylogenetic level.

Assuming a continuance of the complete decussation at the optic chiasma to the tectum, it seems that from Hebb's theory we could have predicted no transfer whatever for the hood-reared birds, since there is no way for the hypothetical intracerebral pathways (phase sequences) necessary for identification of the positive stimuli to have been established by experience. We are nevertheless clearly indebted to Hebb, since his prediction was an important factor in the development of this investigation. On the other hand, from the perceptual theory of Lashley, a complete transfer in the hood-reared birds would have been predicted. This theory does not postulate any experiential involvement of the specific cortical substrate as a necessary condition for transfer of training.

Also, it would appear that neither Lashley's perceptual theory nor Hebb's phase-sequence theory would predict a failure of transfer to the binocular situation after the experimental birds had reached the criterion of learning using each eye individually.

The most economical interpretation seems to be the following: The contrast between an almost 100 per cent transfer from a single eye to the contralateral eye in our normally reared groups and no more than 32 per cent transfer in the hood-reared groups under equivalent test conditions suggests the involvement of differences in perceptual-motor experience between the two groups. Alternative explanations in terms of: (*a*) differences in visual acuity between the normally and hood-reared birds, (*b*) chemical changes in the fluid media of the eyes of the hood-reared birds or changes in retinal photochemistry, as well as retinal and central nervous degeneration in these birds, (*c*) some other structural deficit resulting from the diminished "life style" imposed by hood-rearing, (*d*) differential effectiveness of the pretraining for the hood-reared and normally reared birds, (*e*) qualitative differences between the effectiveness of the reward for the normally reared and hood-reared groups have been previously discussed and rejected by the present author (5, 6).

SUMMARY

An experiment was performed which investigated capacity for transfer of training from an eye uncovered during training to an eye covered in training and to both eyes, using as *S*s ring doves reared throughout life without specific visual form definition. Control groups of normally reared birds were utilized. All groups were first monocularly trained to reach a criterion of nine out of ten correct, consecutive jumps to the positive stimulus in a modified Lashley-type jumping apparatus. Tests for transfer to the contralateral eye or to both eyes were then made. Following this, supplementary testing of the eye used in the original training, or of both eyes functioning simultaneously, was then made. The following conclusions seem indicated:

1. Normally reared ring doves showed immediate transfer of a circle versus triangle discrimination from an eye used in training to an eye which was covered in training.

2. Ring doves reared without specific visual form discrimination (hood-reared) did not show immediate (100 per cent) transfer from an eye used in training to an eye which was covered in training. They did, however, show partial transfer in this situation.

3. More transfer (but not 100 per cent transfer) was seen in ring doves reared without specific visual form definition and trained on a circle versus triangle discrimination from a single eye to both eyes functioning simultaneously than was seen from a single eye to a contralateral eye.

4. Neither of the formal theories here considered would have predicted all these findings.

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TWO TEMPORAL PARAMETERS OF THE MAINTENANCE OF AVOIDANCE BEHAVIOR BY THE WHITE RAT[1]

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A formulation of avoidance behavior offered by Schoenfeld (3) emphasizes three aspects of all successful avoidance conditioning procedures: (*a*) The avoidance response (R_{av}) is never paired with the noxious stimulus. (*b*) All nonavoidance behavior is capable of producing the noxious stimulus and acquiring aversive properties. (*c*) R_{av} is strengthened when it terminates exteroceptive stimulation and/or nonavoidance behavior which has become aversive through pairings with the noxious stimulus.

The critical importance of escape from nonavoidance behavior has been brought out in a series of studies which did not utilize a warning signal (1, 5, 6). In these experiments, however, R_{av}, in addition to preventing the onset of the noxious stimulus, terminated the latter when it did appear. Even this source of strength was eliminated in an experiment by the writer in which no warning signal was presented, and the noxious-stimulus duration was independent of R_{av} (4). The procedure consisted of the presentation of a brief shock at selected intervals, with the provision that any occurrence of R_{av} delayed the shock. No other contingencies between R_{av} and exteroceptive stimulation were involved. The only event which could have signalized the onset of shock was the occurrence of nonavoidance behavior which had previously been paired with shock, and the termination of this behavior presumably provided the reinforcement for R_{av}.

It was noted that continued conditioning with the above procedure produced an avoidance rate which remained stable from day to day. The present experiment was designed to investigate the effects of two temporal variables upon the maintenance of this steady rate.

The independent variables are the durations of the response-shock (R–S) and shock-shock (S–S) intervals. The R–S interval is the period by which each R_{av} delays the shock, or the minimum interval after which a shock can occur following R_{av}. The S–S interval is the time lapse between two consecutive shocks if no R_{av} occurs between them.

On the basis of the three procedural features noted above, certain predictions concerning the effects of these temporal variables are possible. These will be discussed in conjunction with the results presented below.

METHOD

Apparatus

Bar pressing was selected as the avoidance response. The bar, $3\frac{7}{8}$ in. long and $\frac{5}{16}$ in. in diameter, protruded $\frac{1}{2}$ in. into the cage. Approximately 9 gm. of force was required to depress the bar, while a depression of $\frac{3}{8}$ in. closed a microswitch which activated the recording and shock-delay circuits. The experimental boxes, made of galvanized iron, had a floor area of $10\frac{1}{2}$ by 8 in. and an inside height of $11\frac{1}{4}$ in. The floor was a grid composed of $\frac{1}{4}$-in. stainless steel rods $\frac{7}{8}$ in. apart, measured from center to center, a sufficient distance to prevent animal droppings from shorting out the shock. The bar was $4\frac{1}{4}$ in. above the grid. To minimize bar presses resulting from jumping responses, a false ceiling of transparent plastic sloped from the top rear of the cage to a position 2 in. above the bar. Both the bar and the walls of the cage were included in the shock circuit. Grid and bar were sandpapered before each experimental session.

The shock was applied by energizing the 110-v. primary of an 880-v. step-up transformer, and was delivered through a 440,000-ohm resistance in series with the grid. A "grid-confuser," which rapidly alternated the side of the circuit supplying each grid rod, ensured that the animals would receive a pulsating shock regardless of which rods they were standing on. The control apparatus, a system of relays, timers, and associated circuit elements located in the experimental room, did not provide cues for the occurrence of the shock because noises did not occur in any consistent temporal relation to the shock. Timers were calibrated and preset before each experimental session. Illumination was constant during and between experimental sessions.

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[1] This paper is a portion of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Faculty of Pure Science, Columbia University. The writer is indebted to Professors William N. Schoenfeld and Fred S. Keller for their constructive suggestions during the course of this research.

[2] Now with the Neuropsychiatry Division, Army Medical Service Graduate School.

Subjects

Subjects were three male Wistar rats. At the start of experimentation, *S*s 40 and 41 were 275 days old, and *S* 46 was 230 days. At the end of experimentation Rat 40 was 553 days, Rat 41 was 607 days, and Rat 46 was 448 days old. The majority of experimental sessions, each 3 hr. long, occurred on successive days, the animals being run at the same time every day, one animal at a time. Each rat was given several preliminary sessions at different shock schedules to ensure that the rate of avoidance responding was stable before recording experimental data.

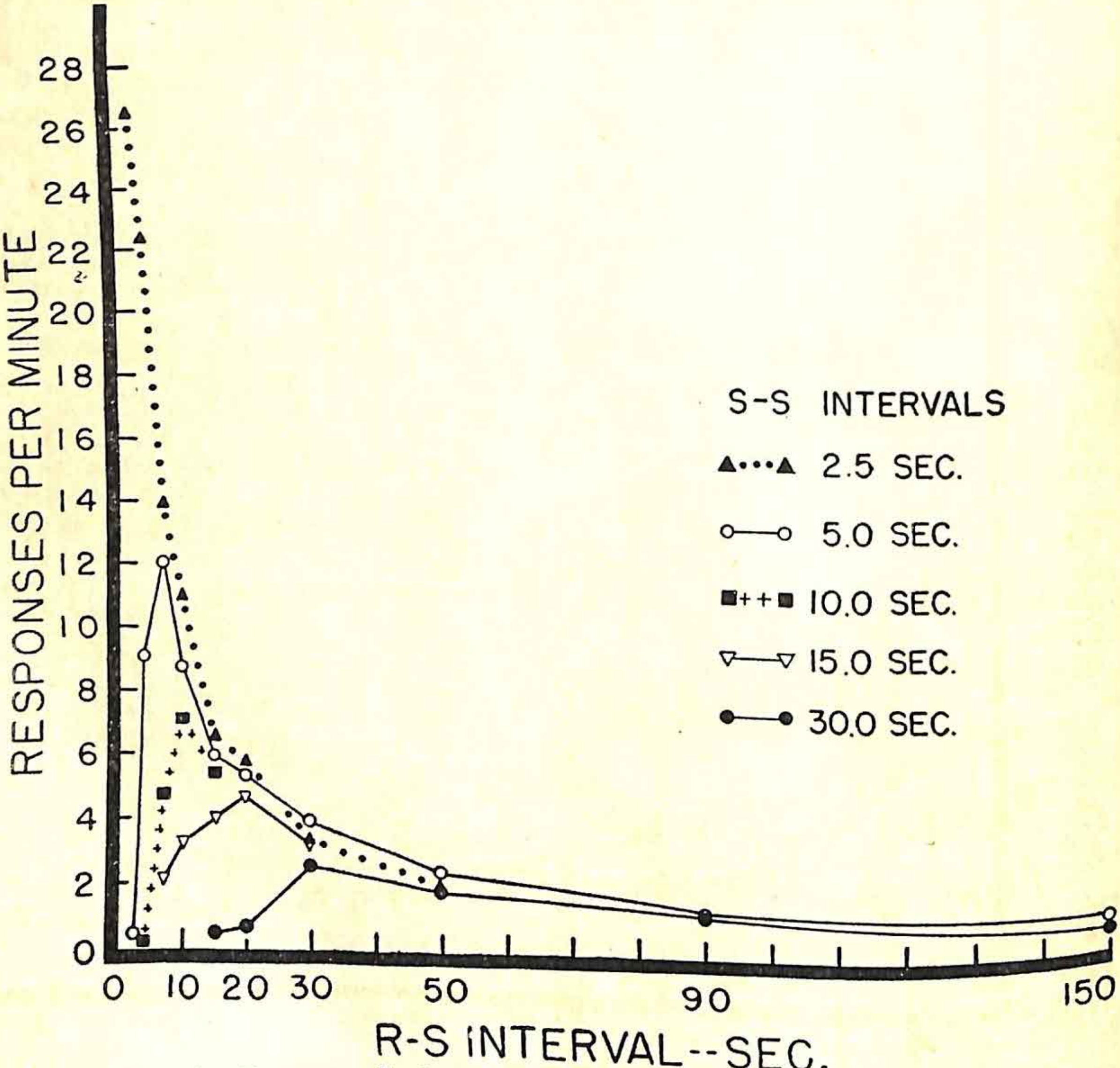

FIG. 1*A*. Rate of avoidance responding by Rat 46, plotted against the response-shock interval, with the shock-shock interval as a parameter

Procedure

The temporal relations involved were the following: shocks were presented at regular intervals as long as no bar-pressing response was emitted. Any occurrence of a bar press, however, delayed the appearance of the next shock for a specified interval after the response. The time between successive shocks if no bar press occurred is the shock-shock (S–S) interval; the interval by which each response delayed the shock is the response-shock (R–S) interval. For example, on a shock schedule of S–S = 15, R–S = 30 sec., shocks occurred every 15 sec. unless a bar-pressing response was emitted. Every bar press delayed the shock for a period of 30 sec. from the response. If a bar press occurred, e.g., 10 sec. after one shock, the next shock would appear 30 sec. after that response, the interval between the two shocks being 40 sec. Additional responses would delay the second shock still further. In this example a minimum interval of 30 sec. is assured between bar depression and shock. Only the initial bar depression

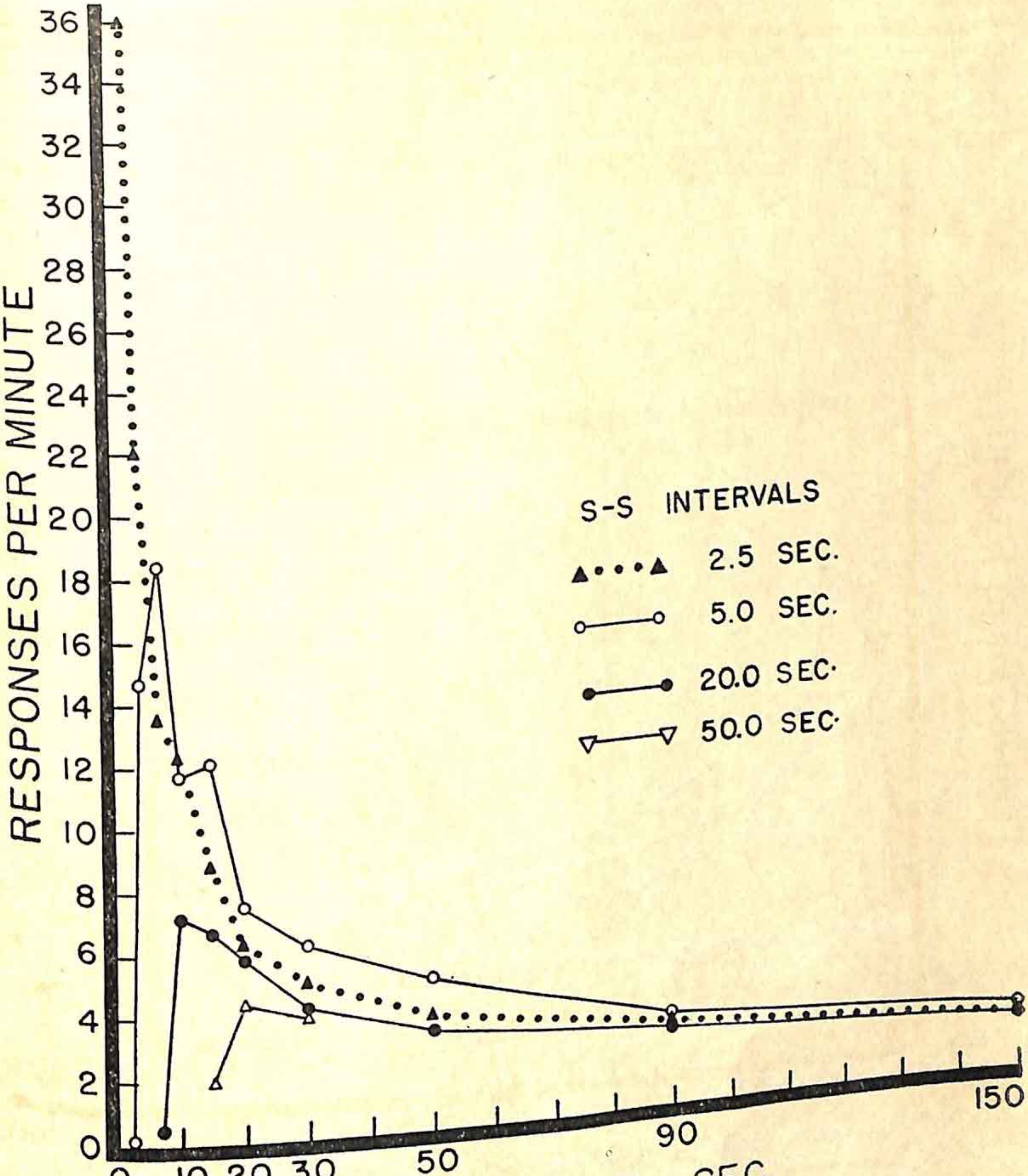

FIG. 1*B*. Rate of avoidance responding by Rat 41, plotted against the response-shock interval, with the shock-shock interval as a parameter

delayed the shock; holding the bar down did not affect the interval. Shocks were of a fixed 0.2-sec. duration.

Experimental Design

Response rates were obtained for each animal at various combinations of S–S and R–S intervals. When enough experimental points were secured to indicate the shape of one rate vs. R–S-interval function, with the S–S interval constant, the S–S interval was changed and another rate vs. R–S-interval function obtained. A family of such curves was generated by each animal. The points on each function were secured in different sequence, and the S–S intervals were presented to each animal in a different order.[3] Of the 138 experimental points comprising the curves, 5 were determined a second time, the second value being utilized in the accompanying data. These few points were redetermined because they were originally so far out of line that their validity was extremely doubtful. In all cases the second value was consistent with the remaining points on the curves.

Each animal was run on a given schedule until a steady rate was maintained. The criterion of steadiness required, before changing from one schedule to another, was a difference in rate not greater than 0.1 responses per minute between any two out of three consecutive sessions. Only the third hour of each 3-hr. experimental period was used in measuring these rates. Response rates presented below are those prevailing during each criterion period.

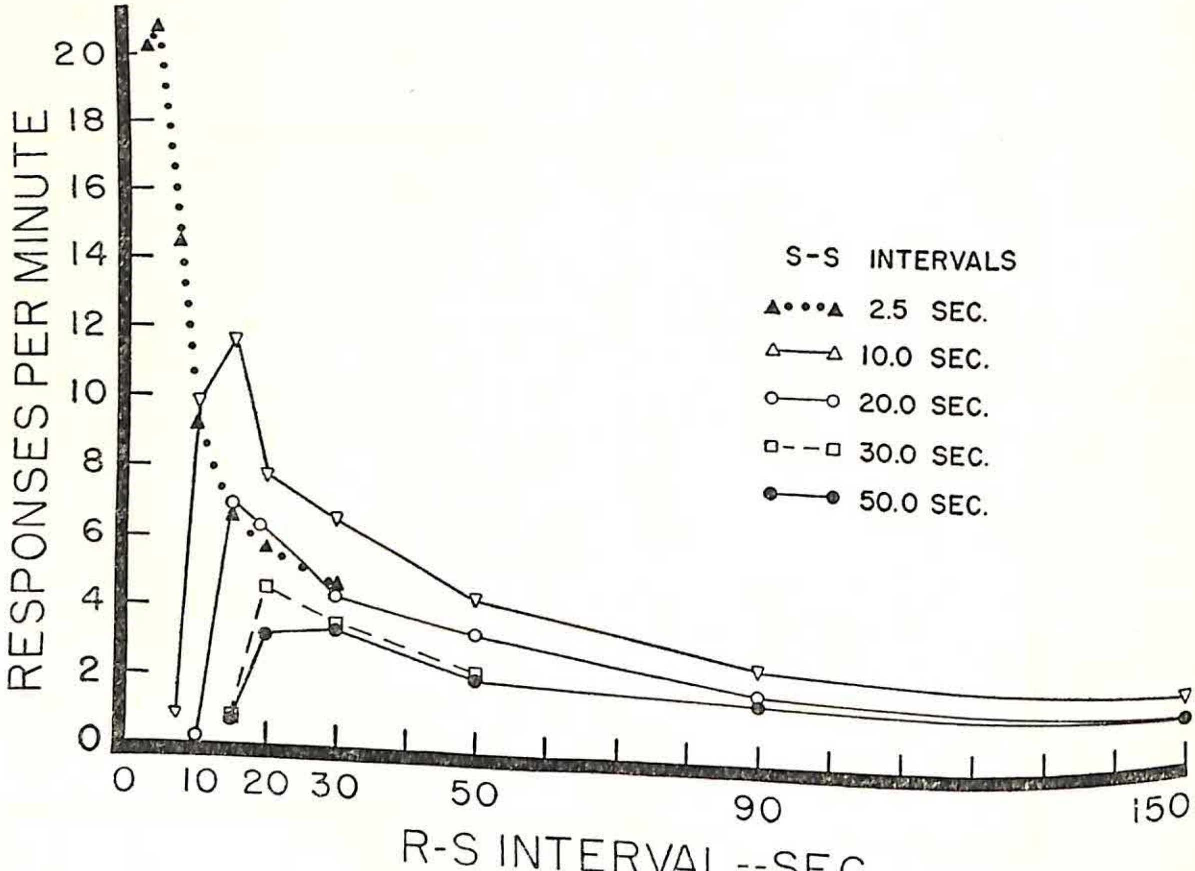

FIG. 1C. Rate of avoidance responding by Rat 40, plotted against the response-shock interval, with the shock-shock interval as a parameter

One reason for discarding the responses of the first 2 hr. was that the length of the "warm-up" period usually observed at the start of each session appeared to be a function of the current schedule. Inclusion of this period would have influenced the average rate differentially at each shock schedule. Second, in changing from a schedule at which a low rate prevailed to one which gave a high rate, and vice versa, the rate adjustment was often complete by the third hour of the new schedule. By utilizing only the responses in the third hour, it became possible to meet the criterion of a steady rate within the first two sessions of a given schedule. The time saving accomplished by this procedure was considerable.

RESULTS

Data relating avoidance rate and R-S interval are plotted in Figures 1*A*, 1*B*, and 1*C*. Only enough of the tabulated rates have been plotted to illustrate the general trends.[4] That each *S* yielded replicative functions with respect to the shapes of the curves can be seen by inspection and is more precisely demonstrated below. Neither the sequences employed for presenting the intervals nor the increasing

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[3] The order of presentation of the shock schedules is contained in Table 1, which has been deposited with the American Documentation Institute. To obtain this table and Table 2, order Document 4017 from ADI Auxiliary Publications Project, Photoduplication Service, % Library of Congress, Washington 25, D. C., remitting $1.25 for microfilm or $1.25 for photocopies.

[4] Tables of the complete data may be obtained from the author.

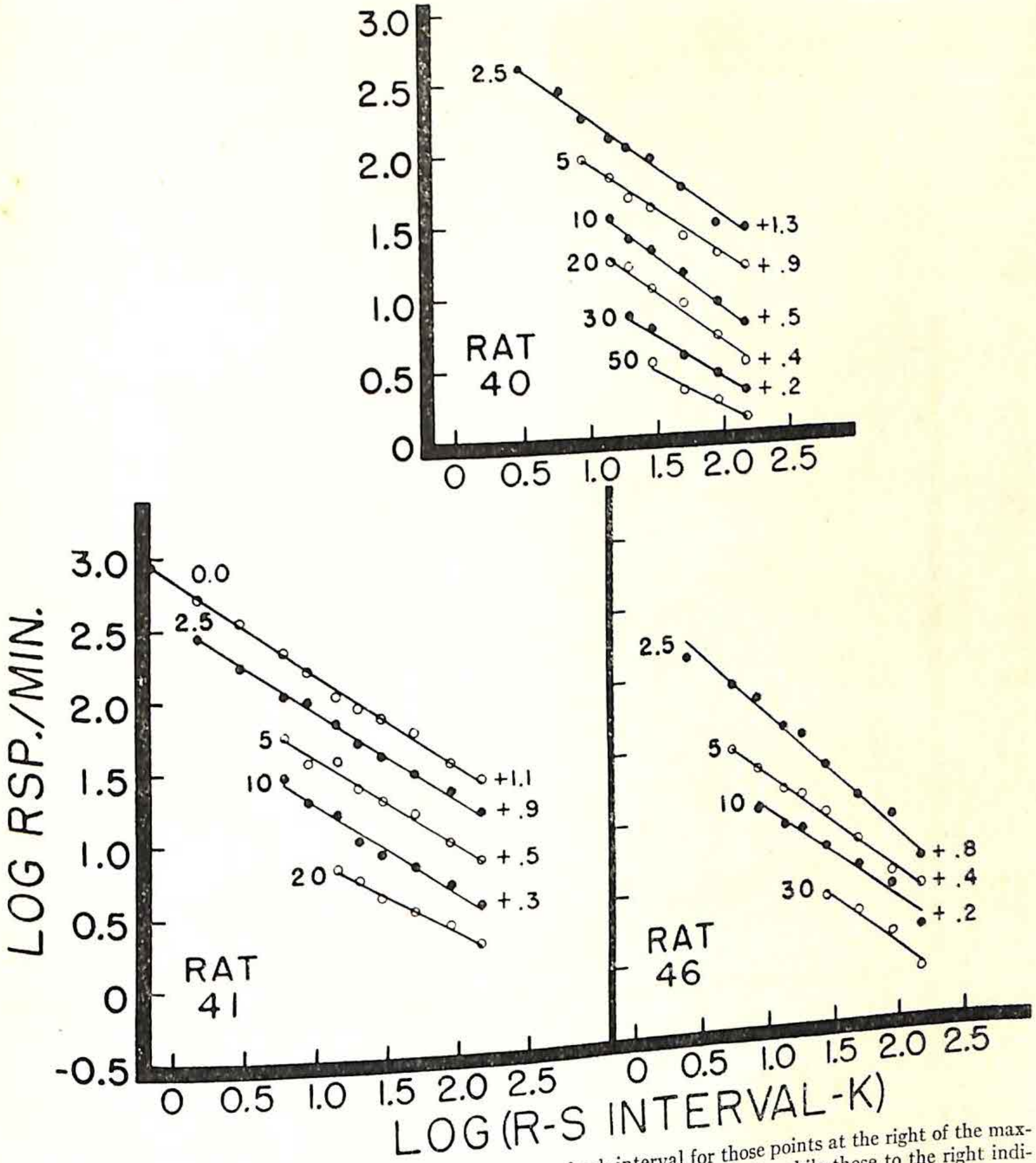

FIG. 2. Log avoidance rate plotted against log response-shock interval for those points at the right of the maxima in Fig. 1. Numbers at the left of each function identify shock-shock intervals, while those to the right indicate the displacement, in log units, of each curve on the ordinate.

ages of the animals affected the orderliness of the data.

As the R–S interval decreases, the avoidance rate increases to a maximum and then falls off rapidly almost to zero at shorter intervals. (Three curves do not show a maximum because the animals did not survive exposure to shorter R–S intervals.) Along with the rates, the number of shocks received in the criterion periods increases as the R–S intervals become shorter.[5] There is no maximum, however, in this function.

In Figure 2 the gradients to the right of the maxima in Figure 1 have been fitted by the method of averages to a logarithmic transformation of the hyperbolic equation,

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[5] Data relating to number of shocks received in the 1-hr. criterion period for each rat and each schedule are contained in Table 2, deposited with ADI. See footnote 3.

$$R = a(t - k)^{-b} ,$$

where R is the rate of avoidance responding, t is the R–S interval, and a, b, and k are constants. The constant k is specific to the organism and independent of the temporal parameters. To obtain separation, the curves have been displaced upward on the ordinate by the indicated number of log units. These curves indicate clearly that the S–S interval plays no part in determining the *shape* of the rate vs. R–S function to the right of the maximum. It may be noted that the zero S–S-interval curve (Rat 41) is of the same shape as the others, even though the zero interval, equivalent to continuous shock, actually provides an escape situation. Bar pressing provides for both avoidance of and escape from the noxious stimulus, but the curve is of the same form as the curves which appear to involve only avoidance.

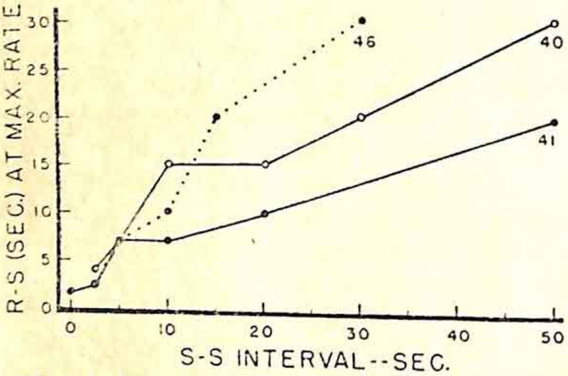

FIG. 3. Response-shock interval at which the maximum rate occurs in each rate vs. response-shock interval function for the three animals

Unfortunately, not enough curves could be obtained to provide an unambiguous picture of the relation between the S–S interval and the constants a and b, though it does appear probable that b remains relatively constant over a wide range of S–S values.

The influence of the S–S interval upon the functions of Figure 1 shows up most clearly at and to the left of the maxima. Although the latter portions of the curves contain too few points to permit a satisfactory mathematical description, certain consistent characteristics may be noted. In each curve there appears to be an R–S interval below which avoidance responding is completely eliminated. Between this interval and the maximum there is a rapid increase in rate. The range of R–S intervals over which the avoidance response is eliminated increases with the S–S interval. Also, as the S–S interval increases, the rise in rate up to the maximum is more gradual. For example, consider the 10-sec. S–S curve of Figure 1*C*. R_{av} is completely eliminated at intervals of zero to approximately 7 sec. The rise to the maximum occupies the intervals from 7 to 15 sec., a range of 8 sec. In the 50-sec. S–S curve, however, the response is eliminated at intervals of zero to approximately 15 sec., while the rise to the maximum occupies the intervals from 15 to 30 sec., a range of 15 sec.

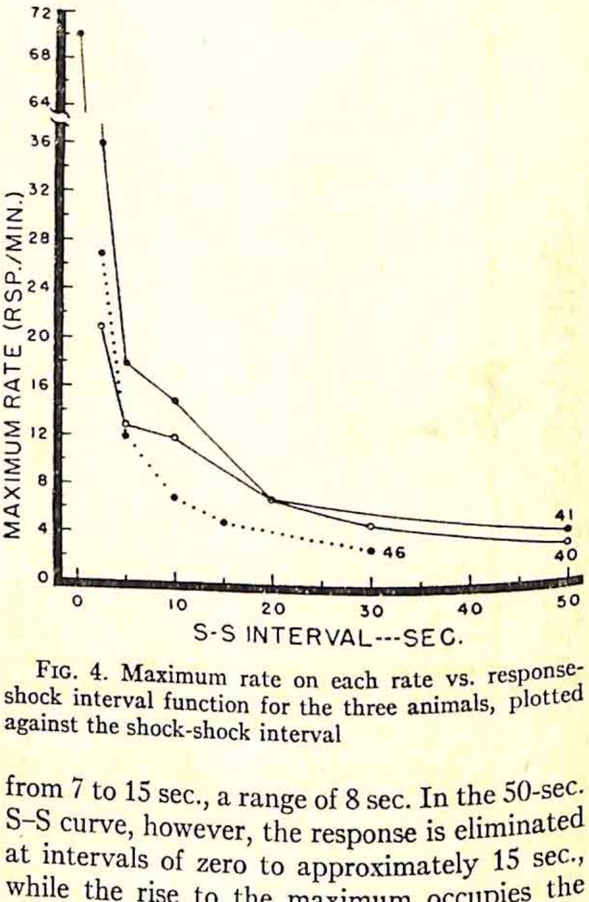

FIG. 4. Maximum rate on each rate vs. response-shock interval function for the three animals, plotted against the shock-shock interval

Figure 3 reveals a relation between the S–S interval and the R–S interval at which the maximum occurs in each rate vs. R–S function. Individual curves show the same general trends, the irregularities probably resulting from the lack of precision in determining the maximum rates, which are specifiable only within a range of R–S intervals. There is little doubt, however, that the function is a rising one.

The maximum rate on each function is

plotted against the S–S interval in Figure 4. Again, despite local irregularities, the functions appear to be of the same type for each animal, the maximum rate decreasing as the S–S interval increases.

Curves relating rate of avoidance responding and S–S interval, with the R–S interval as a parameter, reflect complex interactions among several processes, but are highly consistent among the three animals. Figure 5 will serve as a model for describing the data of all three animals. Again, some points have been omitted in order to make the graph more readable.

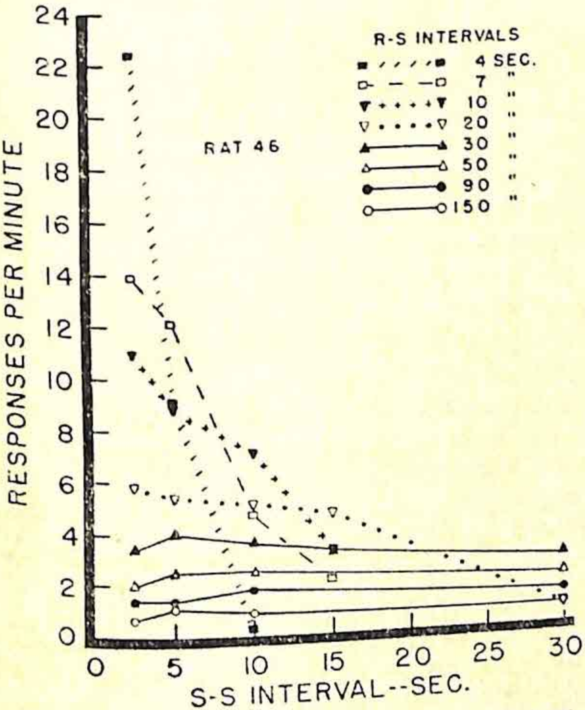

Fig. 5. Rate of avoidance responding by Rat 46, plotted against the shock-shock interval, with the response-shock interval as a parameter

Reading from bottom to top, the height on the ordinate of the four lower curves, ranging from R–S intervals of 150 to 30 sec., shows an inverse relation to the R–S interval at all points. The 20-sec. R–S-interval function maintains this relation out to the 15-sec. S–S interval, after which the curve dips sharply and crosses the lower four. With each succeeding shorter R–S interval, the curves break at a shorter S–S interval. This effect is absent from the curves for R–S intervals ranging from 30 to 150 sec. Very long S–S intervals have little or no influence on the rate of avoidance responding, which is controlled exclusively by the R–S interval. At lower values of the S–S interval, however, there does appear to be a rise in rate in the curves under consideration. It is not clear whether the rate approaches an asymptote or again drops below a maximum, since these portions of the curves are not consistent among the three animals.

DISCUSSION

The curves of Figure 1 can be interpreted in terms of interactions between two gradients, one acting to increase and one to decrease the rate of avoidance responding. The first of these functions may be termed the "distribution-of-punishment" gradient. As the R–S interval is decreased, the frequency of shocks actually received by the animals because of failure to respond in time increases, producing a rise in the probability that any nonavoidance response will be paired with shock. At shorter intervals, then, the behavior terminated by the avoidance response is more likely to be aversive and reinforcements will be more frequent, helping to account for the inverse relation between rate and the R–S intervals to the right of the maximum.

At still briefer R–S intervals, however, R_{av} itself begins to feel the effects of the shock. With a decreasing minimum interval between bar depressions and shock, R_{av} begins to receive occasional pairings with shock. The extent to which R_{av} becomes aversive depends upon the "delay-of-punishment" gradient. The decreasing rates at the left of the maxima may be interpreted as the result of the increasingly preponderant influence of the latter gradient, compared to the distribution-of-punishment gradient.

The effect of the S–S interval upon the distribution-of-punishment gradient shows up most clearly at the maximum. The shifting maximum (Fig. 3) indicates that as the S–S interval increases, the distribution-of-punishment gradient determines a smaller portion of the rate vs. R–S function, relative to the delay-of-punishment gradient. That is, at longer S–S intervals a relatively long delay of punishment of the avoidance response will suffice to decrease its rate without, however, changing the shape of the gradient. By combining these data, which reveal a direct relation between the S–S interval and the R–S interval producing the maximum rate, with those of Figure 2, the inverse relation between the S–S interval and the maximum rate itself (Fig. 4) can be derived. With Figure 3 indicating that the delay gradient "cuts through" the distribution gradient at longer R–S intervals as the S–S interval increases, and with Figure 2 showing an inverse relation between rate and R–S interval, the maximum rate must decrease as the R–S interval containing the maximum increases.

Consideration of the delay-of-punishment gradient, determining that portion of the rate vs. R–S interval at the left of the maximum, reveals more widespread effects of the S–S interval, further supporting the analysis of the data into two separate gradients. The shift in the interval at which the curves rise from near-zero values indicates that the range of delays over which punishment completely eliminates avoidance responding increases with the S–S interval. Also, the changing rate of approach to the maximum indicates that punishment will maintain at least a partial depressive effect over a wider range of delays as the S–S interval increases.

Although short S–S intervals squeeze the delay-of-punishment gradient into a narrow range of R–S intervals, it seems unlikely that the delay gradient could be completely eliminated by further reduction of the S–S interval. This would mean that avoidance behavior could be maintained at high rates with R–S = zero seconds (shock occurring simultaneously with the response). For this reason the constant k was introduced into the equation for the distribution-of-punishment gradient. This constant sets a lower limit upon the R–S interval theoretically capable of maintaining the rate of avoidance responding. Actually, even this lower limit will not be effective, since the above equation demands an infinite rate at an interval of k seconds, a rate obviously not within the organism's capacity. At short intervals, then, there is a "capacity" variable acting with punishment to limit the minimum effective R–S interval. This variable is not represented in the equation because the number of experimental points is not adequate for evaluating the additional constant that would be required.

Further support for the proposal that both escape and avoidance behavior are strengthened by termination of a noxious event (3) is provided by the zero S–S-interval curve (Fig. 2, Rat 41), which involves both escape and avoidance. If these two types of behavior required different reinforcing mechanisms, it might be expected that the zero S–S curve would differ in some respect from the others, but it is entirely consistent.

The discontinuities noted in the curves of Figure 5 result directly from the shifting maxima in Figure 1*A*. For example, if the latter graph is cut vertically at R–S = 20 sec., all points will be on or to the right of the maximum except that on the lower (S–S = 30 sec.) curve, which falls to the left of the maximum. The sudden decrease in rate at the left of the maximum, reflecting the influence of the delay-of-punishment gradient, shows up as a sharp drop in the rate vs. S–S function. The displacement of this break toward lower S–S intervals mirrors the shifting maximum demonstrated in Figure 3. It is evident, then, that at lower values of the R–S parameter, the shape of the rate vs. S–S-interval function is increasingly determined by the delay-of-punishment gradient.

The reason for the absence of this effect in the curves for longer R–S intervals can be found in the relatively small number of shocks occurring at these intervals. Of these few shocks an even smaller number were not followed by R_{av}. Since there was very little difference among the longer S–S intervals with respect to the number of times the S–S interval actually occurred, it was not possible for these intervals to exert a differential effect upon the rate of avoidance responding.

It might be expected that the rise in rate at shorter S–S intervals could be accounted for by an increasing frequency of shocks, as was the distribution-of-punishment gradient. However, examination of Table 2[6] reveals no consistent relation between the S–S interval and number of shocks, with the R–S interval held constant at the values under consideration. The rise in these functions, then, must be attributed to some other factor.

One property obviously correlated with decreasing S–S intervals is the minimum interval between shocks. As this minimum interval decreases, giving a series of discrete shocks a closer resemblance to a continuous one, R_{av} begins to acquire an escape-from-shock function, since its occurrence often terminates such a series. The additional reinforcement provided by this escape function is probably responsible not only for the rise in rate with decreasing S–S intervals, but also for the maintenance of the response rate when the R–S interval is very short—for example, when S–S = R–S = 2.5 sec. As Mowrer and Ullman suggest, "Since the relief obtained by pressing the bar would be immediate and the punishment (more) remote, such behavior might be perpetuated indefinitely" (2, p. 84).

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[6] See footnote 5.

SUMMARY

The present experiment was concerned with the establishment and maintenance of a steady rate of avoidance responding and with variables determining this rate. The effects of two temporal variables were investigated with three white rats: (*a*) the shock-shock (S–S) interval, experimentally defined as the time lapse between two successive shocks if no avoidance response occurred between them, and (*b*) the response-shock (R–S) interval, or the time by which each avoidance response delayed the occurrence of shock. Each animal was run through a series of combinations of these intervals, yielding the following relations and conclusions:

1. Functions were obtained relating avoidance rate and R–S interval, with the S–S interval as a parameter. These curves passed through a maximum, the rate bearing a hyperbolic relation to the R–S interval from the maximum out to the longest interval employed. The shape of these functions was interpreted in terms of two conflicting gradients: (*a*) a delay-of-punishment gradient which operates directly upon the avoidance response to depress its rate, and (*b*) a distribution-of-punishment function which operates to depress nonavoidance behavior which would otherwise compete with the avoidance response.

2. The shape of the distribution-of-punishment gradient is independent of the S–S interval.

3. The R–S interval at which the maximum occurs in each rate vs. R–S function decreases with the S–S interval.

4. The maximum through which each rate vs. R–S function passes increases as the S–S interval decreases.

5. Both the range of delays and the maximum delay at which punishment of the avoidance response depresses its rate increase with the S–S interval.

6. Functions were obtained relating avoidance rate and S–S interval, with the R–S interval as a parameter. These curves assume a shape which depends upon interactions among several variables. As the R–S interval decreases, the functions are increasingly determined by the delay-of-punishment gradient. The effects of the latter gradient are absent from curves for the longer R–S intervals. In these curves the rate at longer intervals is determined solely by the R–S parameter.

7. The higher rates at the shorter S–S intervals and the maintenance of high rates when the R–S interval is very short were attributed to an escape-from-shock function assumed by the avoidance response at short S–S intervals.

8. Each of the three animals yielded functions which replicate those of other animals. Neither the sequences employed for presenting the intervals nor the ages of the animals appeared to be relevant variables with respect to the relations obtained.

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STIMULUS SUBSTITUTION AND RESPONSE LEARNING IN THE EARTHWORM

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Yerkes (3) and Heck (2) studied the earthworm's acquisition of the T-maze habit in which the worm had to learn to turn consistently into one arm of the T and was shocked for entry into the other arm. These studies provide information concerning the modifiability of behavior and the extent of neural differentiation at the phylogenetic level represented by the earthworm. They do not, however, provide sufficient data to enable one to infer the process or processes involved in the behavior changes which occurred during the training or to support the authors' theoretical interpretations of these changes. Yerkes and Heck concluded that the earthworm formed an association between the shock and an originally neutral stimulus located on the shock side of the junction. Heck concluded that learning to take the correct turn was based directly on such an association, i.e., taking the correct turn was a consequence of avoidance of the learned negative stimulus on the incorrect side. Few data are reported, however, to substantiate this interpretation of the learning.

The present investigation consisted of a detailed study of the modifications which took place in the behavior of earthworms as they learned the T maze. As in the Yerkes and Heck studies, the worms had to learn to turn consistently into one arm of the T and received a shock if they entered the other arm. It was hoped that close observation of the changes in the worms' behavior would provide data to test the adequacy of Heck's interpretation of the learning of the maze in terms of stimulus substitution. If this interpretation were found untenable, the data should provide a basis for an alternative theoretical interpretation.

METHOD

Subjects

The *S*s in the present experiment were five earthworms, *Lumbricus terrestris*, obtained locally. They ranged in length from 6½ to 8½ in. The method of housing and transporting *S*s, which is described below, was adopted on the basis of experience with training other groups of worms in a series of earlier, exploratory studies. The method adopted for the experiment reported here minimizes stimulation of the worm in the course of removing it from its living quarters to the maze, and from the maze back to its living quarters after completion of a trial. It was found in the earlier studies that excessive stimulation impaired the worm's performance in the maze.

Apparatus

The *S*s were housed in individual boxes containing moistened earth. The boxes are illustrated in Figure 1. They were constructed so that they could be used as starting boxes and goal boxes. There were two boxes for each worm. At the beginning of each trial one of the boxes was placed at the end of the free arm with the end door open and the cover on. The other box containing the worm was placed at the entrance to the maze and the cover was removed, thus exposing the worm to the light. The boxes contained only a thin layer of earth so that the worm could not avoid the light by burrowing.

A modified Yerkes-type T maze was used. The maze consisted of a rectangular crossbar and a tubular stem of transparent plastic. The stem could be detached from the crossbar easily, thus facilitating cleaning the maze. Copper electrodes were set into the floor at the entrance to each arm. If the worm entered the wrong arm and contacted the electrodes, it received a shock of approximately .06 ma. Figure 2 shows the maze and the position of the electrodes in the maze arms. It was found necessary to provide a cover (not shown in Fig. 2) for the crossbar of the T to prevent *S*s from crawling out of the maze during the earlier stages of the training.

At the beginning of a trial, the worm passed from the starting box to the stem via a wooden channeling device. The broad end of the device was the width of the starting box, and it narrowed down to the diameter of the stem. The walls of the channeling device guided the worm into the stem.

Procedure

The apparatus described above was placed on a 24 by 16-in. wooden base, which was placed on a table in front of a window. Light from the window came from directly behind and above the worm as it progressed up the stem of the T.

The apparatus was prepared for a trial by rinsing all parts with water and lining the floor of the stem and the crossbar with moistened paper toweling which was cut to fit the contours of the maze. The paper toweling provided traction for the worm and protected it from the bare metal of the electrodes in the correct arm. The goal box and the channeling device were then placed in position and the starting box was juxtaposed to the channeling device and the cover removed. If the worm did not leave the box and enter the stem within a few seconds, it was touched lightly with a moistened camel's-hair brush. This procedure was usually successful in inducing the worm to enter the stem. Once the worm had entered the maze, reversing in the stem or backing out was discouraged by the use of a long probe which could be inserted into the stem and applied at the point of maximum effectiveness. No stimulation was applied as long as the worm's anterior end was in the junction, but if there was excessive delay in the stem, slight stimulation of the posterior end was used to get the worm started. A trial terminated when the worm made its way to the goal box. The goal box possessed positive value for the worm as evidenced by its ready entrance into the box once it had reached the end of the correct arm.

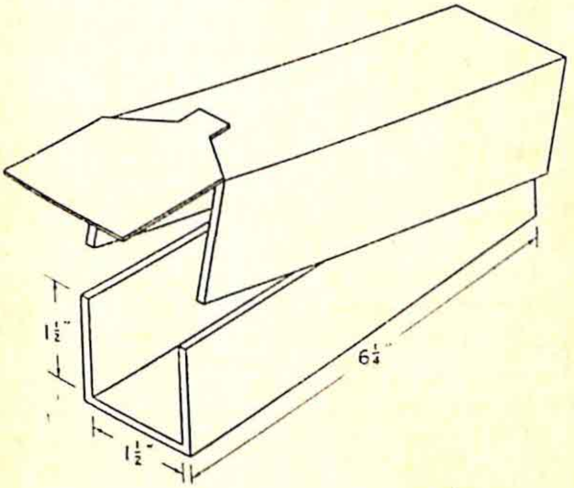

FIG. 1. Design of box used to house earthworms

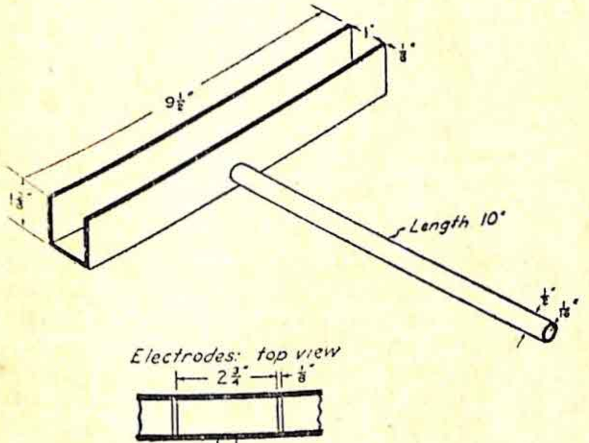

FIG. 2. View of the maze and detail showing position of electrodes

If the worm turned into the incorrect arm, the switch which charged the grid was closed just before the worm contacted it. The shock was made sufficiently strong so that the worm did not pass over the electrodes and down the incorrect arm.

Each worm was given from three to five trials per day. Trials for individual worms were separated by the interval of time it took to run the other four worms. Time per trial and the length of interval between trials varied considerably, as is shown in the following section.

A record was made of the time required by the worm to reach the goal box after entry into the maze stem. Record was also made of the direction of the initial turn in the junction. Only those turns that brought the worm's anterior end to the edge of the grid area on either side were considered in recording initial turns. Mimeographed record sheets were prepared which contained an outline of the maze. The worm's movements during its passage through the maze were recorded in the outline.

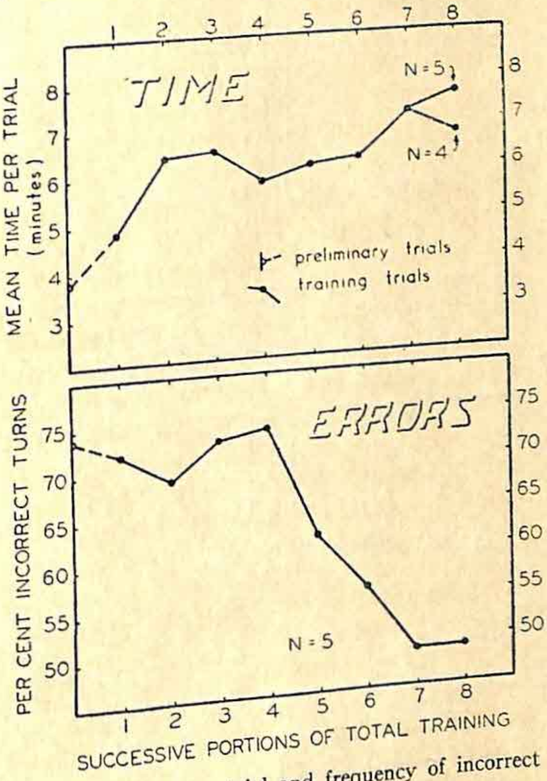

FIG. 3. Time per trial and frequency of incorrect turns at successive stages of training

A preliminary series of 25 trials was given to habituate the worms to the apparatus and to determine their individual turning preferences. Both arms of the maze were free during these trials. During the training trials the worm had to enter the nonpreferred arm and was shocked if it entered the preferred arm.

RESULTS

Figure 3 gives the changes in performance of the worms as a group in terms of time per trial and frequency of errors (initial turns into the incorrect arm). Each point represents the mean of the means for five *S*s for a portion of the training of about 25 trials. The mean values for the preliminary series are also given. The lack of homogeneity in the variability of the performance of *S*s precluded the use of a statistical test based on an assumption of normality, and therefore Festinger's (1) nonparametric method was used to test the significance between the preliminary-series time and error means and the means at the successive stages of training. There is a significant increase in the time per trial by the second portion of training ($p < .01$). The frequency of errors does not decrease significantly until the sixth portion of training ($p < .01$).

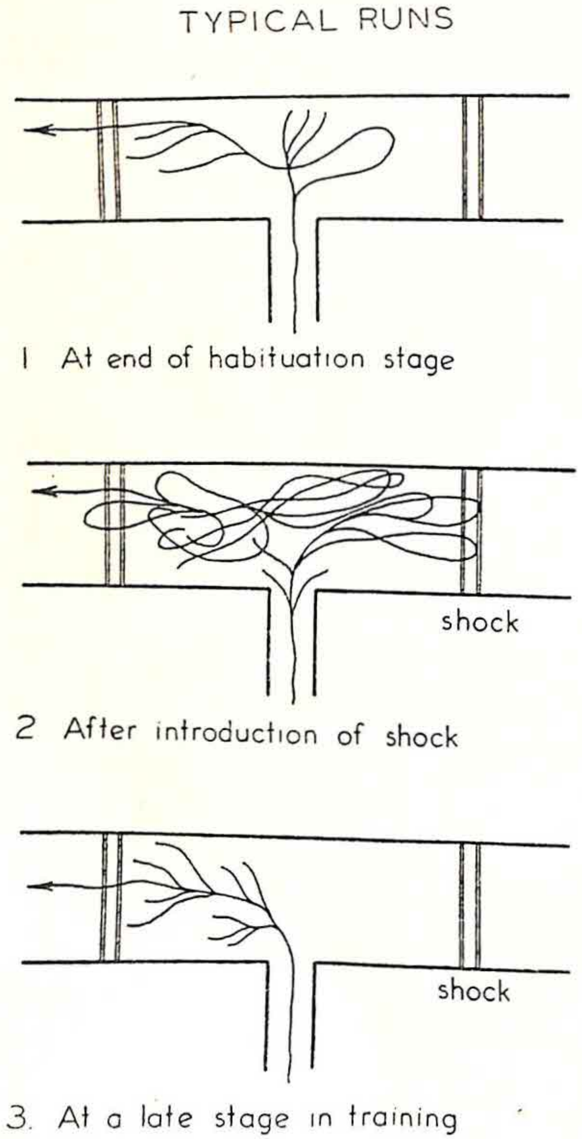
TYPICAL RUNS
1 At end of habituation stage
shock
2 After introduction of shock
shock
3. At a late stage in training

FIG. 4. Tracings from records made of the earthworm's behavior in the maze junction at successive stages in the training

The increase in time per trial took place relatively early in training. After the worm had been shocked on a few trials, it began to show marked negative reactions to all parts of the junction and to the junction entrance. These changes in behavior resulted in an increase in the time required to reach the goal box. Two mean values are given for the final portion of the training. The higher value gives an erroneous impression of a continued rise in the time curve because of the extremely long time required by one *S* to run the maze. The lower value represents the mean when this *S* was not included. The decrease in frequency of errors did not take place until 75 to 100 trials after the increase in time per trial.

Figure 3 shows that learning was not perfect when training was discontinued. Training was not terminated, however, until it appeared that an excessively large number of trials would be required to produce any further change in time or error curves.

Figure 4 indicates the three general stages which were discernible in the learning. In the initial stage, during the preliminary series, the agitation and excess movements which were present at the beginning decreased, i.e., the worm became habituated to the maze situation. The second diagram illustrates the intermediate stage, which appeared shortly after shock was introduced. Stimulation provided by the junction and the stem near the junction elicited sharp retraction responses. Lingering in and near the junction was frequent. There was much vacillation between the two arms before one of them was entered. Stimuli on both sides of the junction elicited negative reactions. Diagram 3 illustrates the final stage. The worm's activities were restricted to the electrode areas, especially the area on the correct side. Some negative reactions, even to stimuli on the correct side, were still made. Lingering in the junction was still present.

The worms persistently reacted negatively to stimuli on both correct and incorrect sides of the junction. Negative reactions to junction stimuli on the correct side of the junction persisted even after entries into the correct arm increased in frequency.

DISCUSSION

The results of the present study indicate that the earthworm's successful performance in the T maze is not based on a precisely localized association. One finding which argues against this interpretation is the long interval (75 to 100 trials) between the appearance of shock-induced negative reactions to junction stimuli and the increase in frequency of correct turns. If the maze were learned on the basis of the avoidance of specifically localized junction stimuli which had acquired negative value by association with shock, the above two changes would have accompanied each other rather than appearing at different times in the training. Also, the negative reactions induced by the shock were not restricted solely to the shock side of the junction, but were made to stimuli on the correct side and to stimuli at the entrance to the junction.

Heck and Yerkes inferred from their observations that an association between shock and some other precisely localized stimulus was gradually built up. The present study also found evidence of the formation of an association involving shock, but the evidence indicates that the association did not develop gradually and did not involve a precisely localized stimulus. The association was formed early in training, and involved indiscriminate negative reactions to stimuli anywhere in the junction.

Two distinct behavior modifications appeared in the course of training: (*a*) increase in negative reactions to junction stimuli and (*b*) increase in frequency of correct turns. A two-factor theory seems best able to account for these results although alternative interpretations are possible. A dual-process theory would account for the development of negative reactions in terms of a conditioning process depending upon contiguity of shock and junction stimuli. The increase in frequency of correct turns would be viewed as mediated by a selective-learning process, i.e., the elimination of incorrect responses to junction stimuli and fixation of the correct response by virtue of differential reinforcement (escape from photic and tactual stimulation, escape from drive-arousing stimuli in the junction).

Earlier interpretations of worm learning in the T maze in terms of simple avoidance of a precisely localized learned negative stimulus do not seem adequate to account for the results of the present study. The shock-induced negative reactions do not appear to be directly related to the learning of the maze. The conditioning stage, however, may have contributed to learning by providing an additional source of motivation and reinforcement, i.e., turning into the correct arm from the junction may have been reinforced by escape from the drive-arousing junction stimuli.

There is no direct evidence that the worms were capable of discriminating between the two sides of the junction, as is assumed in the earlier studies of worm learning. What evidence there is argues against such a capacity for discrimination, i.e., the persistence of negative reactions to both sides of the junction after the worm had been shocked on only one side. It seems more plausible to assume that any learning that occurred took place with reference to the junction as a single undifferentiated stimulus. In the conditioning stage the whole junction became a conditioned stimulus for the negative reactions. In the selective-learning stage the correct-turn response was associated with the junction as a whole. This evaluation of the worm's powers of discrimination makes the slowness of the learning understandable. The worm learned conflicting reactions to the same stimulus situation. In the conditioning stage the junction became a cue for withdrawal, and in the selective-learning stage it became a cue for forward progress and turning in a particular direction. The first learning constituted a barrier to the learning and performance of the second response.

Additional evidence of the low level of the earthworm's discriminatory powers was obtained in a number of studies which were made prior to the one reported here. In one of these studies, an attempt was made to test directly the worm's capacity for forming an association between stimuli. The worm had to learn to use a smooth plastic bar which was placed on the junction floor in front of the correct arm as a cue. The position of the bar was varied from left to right and was always on the side free of shock. The worms crawled over the bar readily in the habituation series, but showed strong negative reactions to it after shock was introduced into the situation. The worms showed no signs of learning the discrimination even after extensive training.

An attempt was also made to train worms in the simple turn problem with the plastic bar always on the correct side of the junction. Learning in this situation was very slow in spite of the enhancement of the difference between the two sides of the junction provided by the plastic bar.

The results of the above studies substantiate the conclusions reached concerning the results of the study reported here. After shock has been introduced, the worm associates the shock with the whole junction rather than with the particular aspect of the junction containing the shock. The plastic bar merely constituted an additional source of stimulation in the junction. The worm's negative reactions, once the junction had been associated with shock, were more frequent when the bar was in the junction than when the sides of the junction were not differentiated by the bar.

There is a possibility that the negative reactions to the junction are due to sensitization of the earthworm to junction stimuli by shock rather than to conditioning. Interpretation of these reactions in terms of sensitization seems unlikely in view of the fact that the negative reactions to junction stimuli appeared after intervals of 24 to 48 hr., in which no shock was received. An attempt is now being made to obtain conditioning in the earthworm, and if it is found that conditioning is relatively easily obtained when control for sensitization is included in the experimental design, the conditioning interpretation of the negative reactions to junction stimuli will be strengthened.

SUMMARY

Five earthworms (*Lumbricus terrestris*) were trained to turn consistently into the nonpreferred arm of a T maze. The worm was shocked if it entered the preferred arm. In the course of training two modifications of behavior appeared: (*a*) an increase in negative reactions to stimuli on both shock and nonshock sides of the junction and (*b*) a decrease in frequency of entries into the arm of the maze containing shock. The first change, as measured by an increase in time per trial, appeared relatively early in the training (approximately trial 50). The second change was not statistically significant until trial 150.

It is difficult to reconcile Heck's interpretation of earthworm learning in the T maze, which is discussed above, with these findings. This study provided no evidence of the development of a precisely localized association or a pattern of avoidance of the shock side of the junction based on this association.

A more adequate interpretation can be made by assuming that modifications of the earthworm's behavior took place with reference to the junction as a whole, and that there were two relatively discrete phases in the learning. The first of these is a conditioning phase which occurs early in training and results in the development of diffuse negative reactions to the junction. The second is a selective-learning phase which occurs later in training. During this phase there is a reduction in the frequency of entries into the incorrect arm and an increase in frequency of entries into the arm leading to the goal box. The slowness of the learning to turn consistently into the correct arm may be explained in part by assuming that the junction becomes a cue for two incompatible responses, i.e., withdrawal versus forward progress and turn in a particular direction. The precise relation between the two phases of the learning, however, can only be determined by further experimentation.

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THE EFFECTS OF A CHANGE FROM DISTRIBUTED TO MASSED RESPONSES

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In the study of the effects of massed versus distributed learning trials, primary emphasis has been placed on the relative efficiency of learning under various conditions of trial spacing. While this is an important problem, an equally important and perhaps more practical problem has been largely ignored. Suppose, for example, that conditions require that responses be massed after initial learning. It is conceivable that the response might be learned more efficiently in distributed than in massed trials. If, however, the change from distributed to massed trials results in some decrement in performance, it may be more efficient in the long run to have the original learning in massed trials.

This problem may be approached theoretically through Hull's *Principles of Behavior*, among which the construct of *stimulus trace* is particularly useful (2, p. 11). All stimuli, including response-produced stimuli, are assumed to produce perseverative effects within the organism. In massed trials these effects become a more or less important component of the stimulus situation in which the response is made, depending on the ordinal position of the trial in the series and on the interval between trials. It may be further assumed that such stimulus traces are cumulative over more than one trial but that a point is eventually reached at which the cumulative effect of such stimulus traces becomes constant. In suitably distributed trials, on the other hand, such stimulus traces may be negligible or nonexistent.

Now suppose that one has two groups of *S*s which have had equal amounts of training, one by distributed and the other by massed trials. Suppose further that the number of trials was sufficiently great so that for the massed-trials group most of the learning has been with a constant cumulative stimulus trace. A new block of reinforced trials is begun with the trials being massed for both groups. The group previously trained in massed trials (Group M-M) should show an immediate drop in efficiency of performance because of the absence of the cumulative stimulus trace at the onset of the final block of massed trials. However, there should be a relatively rapid recovery, the number of trials required for recovery depending on the number of trials required to re-establish the constant cumulative stimulus trace.

What about the *S*s trained originally in trials so distributed that stimulus traces could not perseverate from one trial to the next? For this group (Group D-M) the gradual accumulation of stimulus traces in the final block of massed trials progressively changes the stimulus situation from that in which the original learning occurred. According to Hull's principle of response generalization (2), there should be a gradual decrease in efficiency of performance, a minimum being reached when the cumulative stimulus trace becomes constant. This point should correspond in terms of trials with the point of recovery for Group M-M. If reinforcement of response continues, there should be a gradual increase in efficiency of performance from this point as *S*s learn to respond to a stimulus situation which includes a constant cumulative stimulus trace.

In the present experiment "efficiency of performance" will be evaluated in terms of two different criteria, probability or percentage of correct response and latency of response.

METHOD

The basic procedure up to the point of the final block of massed trials has been described in detail elsewhere (1). This experiment involved a total of 44 male albino rats which were 80 to 100 days old at the beginning of the experiment. Preliminary training involved the reinforcement of two different responses in a modified Skinner-Youtz apparatus. One response was elicited and rewarded 45 times in blocks of 20, 20, and 5 trials. This was designated R', the false response. The alternative response was elicited and rewarded 10 times in a single block of massed trials following the first block of 20 trials for R'. This alternative response was designated R_c, the correct response.

The second stage in training was to place *S*s in a situation where either response could be made, but where only R_c was rewarded. The method of training was noncorrectional, that is, either response, whether rewarded or not, constituted a trial. The 44 *S*s were divided into two groups of 22 each, the groups being equated in terms of latency of response in preliminary training. One group, M-M, made 100 responses in a single block of consecutive massed trials. Group D-M made 100 responses in this situation with an interval of not less than 24 hr. preceding each response.

The third stage in training was similar to the second, excepting that the 50 responses elicited were in consecutive massed trials for both groups. Group M-M thus had a block of 100 massed choices between R^f and R_c followed by a second block of 50 massed choices. Group D-M had 100 distributed trials in which they could make either the R^f or R_c response followed by a single block of 50 massed trials.

Latency of response was measured by stop watch from the time a shutter exposed the manipulanda for the two responses to the time either manipulandum was moved sufficiently to make an electrical contact. In the results to follow, latency of response is the latency for each group of 22 *S*s, regardless of whether the response made was R^f or R_c. Percentage of correct response is the percentage of each group making the R_c response on a given trial.

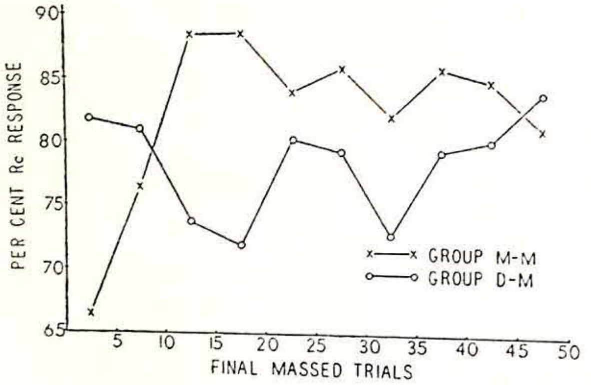

FIG. 1. Percentage of R_c response in final massed trials training, each point representing percentage R_c over five trials

RESULTS

Percentage of Correct Response

In Group M-M 81.8 per cent of *S*s made the R_c response on the last trial of stage-2 training, and 59.1 per cent made this response on the first trial of stage-3 training. The difference is 22.7 per cent. The procedure suggested by McNemar to determine the significance of a difference in percentages for correlated measures (4, p. 80) yields a value of 15.1 per cent for the standard error of the difference, t equals 1.53, and p equals .063. Although the difference between trials is in the direction predicted, the difference cannot be considered statistically significant at the .05 level of confidence.

Figure 1 presents graphically the percentage of R_c responses for Group M-M over the final 50 massed trials. Inspection indicates a rapid increase in the percentage of correct responses over the first 15 to 20 trials, followed by a gradual decrease over the final 30 trials.

In Group D-M 77.3 per cent of *S*s made the R_c response on the last trial of stage-2 training, and 90.7 per cent made this response on the first trial of stage-3 training. Although the distribution of responses does not permit use of the statistical test mentioned above, it would appear unlikely that the difference in percentages is statistically significant. It should be noted, however, that for Group D-M the percentage of correct response is greater on the first trial of the final block of massed responses, whereas for Group M-M the percentage of correct response is greater for the final trial in stage-2 training.

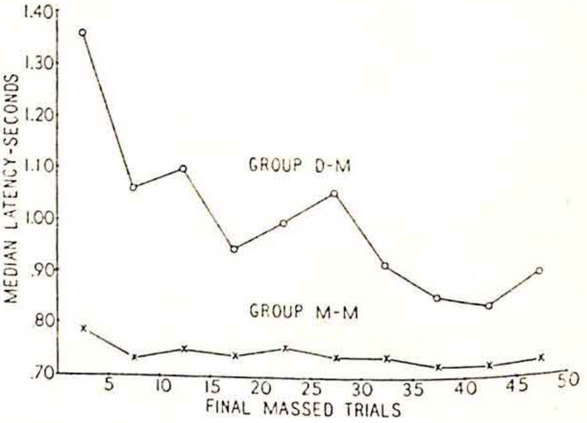

FIG. 2. Median latency of response (in seconds) in final massed trials training. Latencies for five trials were combined in computing medians.

Figure 1 shows that there is a relatively rapid decrease in percentage of correct responses for Group D-M over the first 20 trials of the final block of massed trials. This decrease corresponds approximately with the increase in percentage of correct responses for Group M-M in terms of the number of trials involved. Following this decrease, Group D-M shows a gradual but irregular recovery in percentage of correct responses. The maximum difference in percentage of R_c response for Group D-M in the final 50 massed trials is between trials 16 to 20, where the mean percentage of R_c is

71.8 per cent, and trials 46 to 50, where it is 83.6 per cent.

Latency of Response

For Group M-M the mean difference in latency between the last trial of stage-2 and the first trial of stage-3 training is .40 sec., with latency greater for the first trial of stage 3. The standard error of the mean difference is .31 sec. The value of t is 1.29 with p equal to .098. The mean difference in latency cannot be considered significantly different from zero. Figure 2 indicates that, except for the median latency of the first five trials of the final block of massed trials, the median latencies of response for Group M-M are relatively constant.

Group D-M shows a mean difference in latency of response between the last trial of stage-2 training and the first trial of stage-3 training of 1.15 sec. The direction of difference is toward greater latency on the first trial of massed training. The standard error of the mean difference is .63, t equals 1.83, and p is .033. The mean difference in latency can thus be considered significantly different from zero.

Figure 2 shows an irregular but generally downward trend in median latency of response throughout the final 50 massed trials for Group D-M.

DISCUSSION

Insofar as percentage of correct responses is used as a criterion of performance, the theoretical expectations advanced in the introduction appear to be justified. The fact that Group M-M shows a sharp decrease in percentage of correct responses at the outset of the final block of massed trials while Group D-M does not is compatible with the theory advanced, although the results do not attain statistical significance. It would appear further that in these particular circumstances a constant cumulative stimulus trace is attained at approximately trial 20 in the final massed block, as indicated by the records of both groups.

There is some suggestion from Figure 1 that Group M-M may have been gradually decreasing in percentage of correct response while Group D-M was gradually increasing in this respect during the latter part of the final 50 massed trials. A more extended block of massed trials would be required to substantiate this suggestion. If substantiated, it would point to the superiority of distributed over massed initial training even when later performance is to be under massed conditions of response, at least so far as correctness of response is concerned.

The outcome of the experiment in relation to theoretical expectation is quite different when latency of response is considered. Group M-M suffers only a minor decrement in performance at the beginning of the final session of massed trials while Group D-M undergoes a statistically significant loss of efficiency. The outcome is the reverse of that expected. Also contrary to expectation is the finding that Group D-M shows an irregular but generally decreasing latency of response throughout the entire 50 massed trials. Theoretically one would have expected a gradual increase in latency followed by a decrease.

In interpreting the latency data a factor of possible importance is the difference in age between *S*s of Group D-M and of Group M-M. At the beginning of the final massed training trials *S*s of Group D-M were approximately 250 days old while *S*s of Group M-M were about 140 days old. Such an age difference might tend to increase the absolute differences in latency between the two groups by making latencies greater for the older (D-M) group. There is no obvious reason for supposing, however, that this age difference could account for the differences in the form of the learning curve between the two groups or for the differences between the empirical curves and those predicted.

The recent appearance of Hull's book, *A Behavior System* (3), suggests another application of the data presented here. Theorem 8 states: "Tests applied 24 hours after the completion of a given amount of learning will show, other things equal, that distributed-trials learning is more efficient than massed-trials learning, though the advantage is not as great as will appear during the learning process" (3, p. 37). The data of the present experiment fail to confirm the latter part of this expectation. In terms of percentage of correct response, Group D-M *S*s show a greater superiority to Group M-M *S*s on the first trial of the final stage of training than on the last trial of the preceding stage. (The latency data would appear to refute the theorem in its entirety but are of questionable validity in this respect because of the age differences mentioned above.)

In the derivation of his Theorem 8, Hull was primarily concerned with the dissipation of reactive inhibition over an interval of time. He did not use the construct of stimulus trace in his predictions concerning the differences between massed and distributed learning. The results of this experiment would suggest that this is a significant omission in his derivations.

SUMMARY

Forty-four male albino rats were trained to make two different responses in a Skinner-Youtz apparatus. They were then divided into two equated groups. One group made 100 massed choices between the two responses with only one being rewarded, followed by a second block of 50 massed choices. The other group made 100 distributed choices followed by a block of 50 massed choices. The first group tended toward a decrease in the percentage of rewarded responses at the outset of the final block of trials but recovered in 15 to 20 trials. The second group showed a gradual decrease in percentage of rewarded responses over the first 20 trials of the final massed block, followed by a gradual increase. In terms of latency of response, the first group showed a fairly constant latency throughout the final 50 trials. The second group showed a significant increase in latency at the outset followed by a gradual decrease.

The experimental situation was discussed theoretically in terms of Hull's principles of behavior, and the construct of a constant cumulative stimulus trace was introduced. This modification of Hull's own theoretical derivation appears to fit the experimental findings with regard to "correctness" of response reasonably well. The problem of predicting latency of response appears to be more complicated.

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A MORE SENSITIVE TEST OF IRRELEVANT-INCENTIVE LEARNING UNDER CONDITIONS OF SATIATION

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The major criterion of irrelevant-incentive learning used in the Iowa-type latent-learning experiments (5, 10, 11) has been change in performance accompanying a shift of motivation from the training trials to the test trials. A significant change in the performance on the first test trial, in the direction of selecting the pathway leading to the commodity for which *S*s were then motivated, was accepted as evidence that irrelevant-incentive learning occurred. There was, however, no knowledge available as to what a shift in motivation would produce without *S*'s having had any opportunity for irrelevant-incentive learning to occur. Recently, Kendler and Levine (6) and Kendler, Levine, Altchek, and Peters (7) have reported that about 50 per cent of their *S*s, after having learned to go to the food side of a T maze for 12 successive correct responses, switched their spatial response when their motivation was shifted to a relatively strong thirst drive. In their experiments the end box on the side to which *S*s switched was *empty* during the training trials, and consequently the change in *S*s' performance appears, at least to some extent, to be a function of the shift from one drive to another.

The above would suggest that a greater emphasis be placed upon other criteria of irrelevant-incentive learning. Kendler (2) in an unpublished study used a "learning criterion" of irrelevant-incentive learning under conditions of satiation. He trained two groups of satiated *S*s in a T maze. The first group found food in one end box and water in the other. The end boxes for the second group were empty. The test series consisted of daily trials during which time *S*s were either hungry or thirsty, and food and water were in the same position as they had been during the training series for the first group. Presumably, if the first group had learned anything about the location of the food and water when they were satiated, they should be able to respond more appropriately during the test series, i.e., choose the food side when hungry and the water side when thirsty. It was found that the first group achieved a criterion of learning (four successive appropriate responses) during the test trials significantly faster ($p = .05$) than did the second group. At first glance, such evidence would seem to indicate that the first group demonstrated irrelevant-incentive learning, i.e., their superior performance during the test trials must be attributed to their learning the locations of food and water during the training trials. A more careful analysis of the above experiment would reveal, however, that such a conclusion does not necessarily follow. Kendler's experimental design fails to separate the effects of the *presence* of the irrelevant goal objects during the training trials from the effects of their *location*.

It could reasonably be argued that initially both groups were making emotional responses in the T-maze situation, but these responses subsided more rapidly in the first group since responses incompatible with these emotional responses were evoked by the food and water (1). If such were the case, then the faster learning of the first group during the test trials could be attributed to their lower emotionality rather than to any irrelevant-incentive learning which had occurred during the training trials, i.e., the superiority of the first group was due merely to the presence of the irrelevant goal objects during the training trials rather than to their specific locations.

An experimental technique capable of isolating the effects of the presence vs. the location of the irrelevant goal objects would involve duplicating Kendler's experiment with the addition of a third experimental group: one that would find food and water in the end boxes during the training trials, but in a location opposite to that which would exist during the test series. Any difference during the test series between the performance of this group and the group having the food and water in the same place during the training and test series could be attributed to the differential effects of the location vs. the presence of the food and water during the training series. This paper reports the results of such an experiment.

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METHOD

Subjects and Apparatus

The *S*s for this experiment were 30 naive male albino rats purchased from the Albino Farms, Red Bank, New Jersey. At the beginning of the experiment they were approximately 80 days old. A single-choice T maze, a description of which is given in a previous paper (3), was used. In this experiment, the entire maze was painted a flat gray.

Procedure

Preliminary training. All *S*s were handled for about 5 min. daily for approximately one week prior to the experiment proper. On the first day of the experiment, five *S*s were placed simultaneously in the maze and allowed to explore freely for 1 hr. During this time, all doors were raised. On the next day, *S*s were tested for position preference. Each *S* was given three free-choice trials. No animal used in this experiment chose the same side on all three trials.

Training series. During the training series, all *S*s were satiated for both food and water. The procedure used to induce satiation was to have food and water present in the home cages for the 2 hr. following the daily trials, at the end of which time the food and water were removed. Four hours before the experimental trials, the water and food were replaced in the home cages. One hour prior to the trials, a dish of powdered food was placed in the cages.

The *S*s were randomly divided into three groups of ten *S*s each. The maze situation differed for these groups during the training trials. There was no food or water in either end box for group O, while Group C had a dish of water present in the left end box and six pellets of Purina Laboratory Chow in the right end box. The maze conditions for Group R were opposite those for Group C; the water was in the right end box and food in the left end box.

The training series consisted of four daily trials for seven days. The initial run of each day was free choice, the second was a forced trial to the side opposite that chosen on trial 1, the third was free choice, while the fourth was a forced trial to the side opposite the choice of trial 3. The *S*s were kept in the goal box on both free and forced trials for a period of 30 sec. There was no evidence of any *S*'s eating or drinking during the training trials.

Because of the sluggish condition of *S*s, induced by the satiation procedure, it was decided that a gentle push would be administered if an *S* remained in one spot for more than 5 min. This procedure, which had been used in a previous study (5), produced no observable emotional reactions (defecation, urination, freezing) in *S*.

Test series. The procedure, as well as the maze situation, was similar for all groups during the test series. Each *S* was given a single daily trial beginning on the day following the last day of the training series. On the first and fourth days of the test series, *S*s were motivated by a 22-hr. hunger drive, while on the second and third days, *S*s were motivated by a 22-hr. thirst drive. This *abba* alternation was continued for a period of 17 days.

The maze conditions which prevailed for Group C during the training series (water on the left side and food on the right) prevailed for all groups during the test series. Group C had constant maze conditions during the training and test series, while for Group R the situations were reversed. Group O, it will be recalled, did not have any food or water in the maze during the training series.

During the test series, if an *S* responded appropriately, it was permitted to eat for 20 sec. or drink for 5 sec. If an *S* responded inappropriately, it was detained in the end box for a period of 30 sec. The *S*s in all groups received daily test trials until a criterion of four successive correct trials was achieved or until they completed 17 test trials.

TABLE 1

Number of Trials to Reach Criterion of Learning during Test Series

GROUP	MEAN	σ	MEDIAN	RANGE
C	2.4	2.9	2.0	0–10
O	5.3	2.6	5.0	0–10
R	13.9*	4.4*	17.0	4–17

* Six of the ten *S*s in Group R failed to achieve the criterion of learning during the 17-trial test series. The mean and standard deviation of this group were determined by assigning a score of 17 to these six *S*s.

RESULTS AND DISCUSSION

The performance of the three experimental groups was quite similar during the training trials; the percentage of their free-choice responses to either side tended to fluctuate about the 50 per cent level. The performances of these groups during the test series, however, were markedly different. Table 1 presents the mean and median number of trials (not including the criterion trials) required by each group to achieve the criterion of four successive correct trials. The distributions of the scores of both Groups C and R were highly skewed, and consequently the comparisons between the means of the various groups were made with the use of the *U* test (8). It was found that on the basis of a two-tail test, the differences between Groups C and O, O and R, and C and R were significant at the .02, .01, and .001 levels, respectively.

The results refute the hypothesis which instigated the present research. If Kendler's results (2) could be attributed to the mere presence of irrelevant goal objects during the training trials, then it would be expected that no difference between the performance of

Groups C and R should occur during the test trials. The fact that this difference did occur, as well as the fact that Group C's performance was superior and Group R's performance inferior to Group O, would seem to provide definite evidence that satiated *S*s are capable of learning the position of irrelevant goal objects.

On the theoretical level, the results do not contribute anything new. Spence (10) has provided an S–R explanation of irrelevant-incentive learning, with the use of the concept of the fractional anticipatory goal response, which is capable of explaining the present results. The cognitive theorist's explanation would be based upon the assumption that expectations as to the location of the food and water were formed during the training trials.

The marked retardation in the performance of Group R during the test series raises some interesting questions. Previous studies (4, 9, 10) have reported relatively slight degrees of irrelevant-incentive learning under conditions of satiation. Why, it may be asked, does Group R evidence such poor performance? According to an S–R explanation, the inadequate performance of Group R would be attributed to the assumption that the cues produced by the fractional anticipatory eating and drinking responses become connected to the "wrong" spatial responses. One possible reason why these inappropriate associations did not become extinguished more rapidly is that they always led to some secondary reinforcement, since food or water was always present following an inappropriate test response. Such a possibility could easily be tested.

Another question raised by the present results is whether the retardation demonstrated by Group R is inordinately great. Would *S*s that were motivated for both food and water during the training trials have as great difficulty as did Group R in learning the position of the food and water when reversed during the test series? According to Spence's analysis (10), they should have even greater difficulty.

It appears, therefore, that the major theoretical significance of the present study is in the questions it raises rather than the answers it provides.

SUMMARY

Three groups of white rats were trained in a T maze when satiated for food and water. Both end boxes were empty for Group O, while food was in one end box and water in the other for Groups C and R. During the test series, the *S*s received daily trials under conditions of food or water deprivation. The location of the food and water was the same for all groups, being in the positions that prevailed for Group C during training, while being reversed for the *S*s in Group R, i.e., if food had been in the left end box during training, it was placed in the right end box during the test series.

It was found that Group C achieved the criterion of learning (four successive correct responses) most rapidly. The performance of Group O, although significantly poorer than Group C, was significantly superior to Group R. The results of the performance of the three groups provided marked evidence of irrelevant-incentive learning under conditions of satiation.

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LATENT LEARNING AS A FUNCTION OF THE NUMBER OF DIFFERENTIAL CUES

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We may think of latent learning as the acquisition of "cognitive maps" under conditions which provide no opportunity for an immediate manifestation of the influence of such "maps" upon goalward behavior; or as the acquiring of those perceptual responses which, when accompanied by an appropriate motive, mediate a less random performance than would be possible without the perceptual preparation. Whatever terminology one may prefer, present formulations appear to be in agreement with the general proposition that latent learning is a process which depends upon certain conditions of stimulation for its inception and has its criteria in subsequent behavior.

We hope to maintain the distinction between latent learning and irrelevant-incentive learning presented by Thistlethwaite (9) because attempts to study motive-incentive relations and latent learning simultaneously seem to lead to abstruse problems of interpretation. For this experiment, the term "latent" is used to represent that learning which may occur in a multiple-T maze during exploratory periods which do not include any known source of differential reinforcement. To qualify as latent, this learning must enable the groups of rats that have explored the maze to perform, on an experimentally motivated test trial, in a manner superior to that of a control group which has not had the exploratory experiences. Superior performance may be shown in terms of (*a*) number of errors made at choice points, (*b*) depth of entrance into culs, and (*c*). the time between entry into the start of the maze and entry into the goal box.

Recent evaluations of research by Hilgard (2), Munn (6), and Thistlethwaite (9) support the belief that there is a critical need for a more complete analysis of the conditions of the perceptual field within which this kind of learning may occur.

THE PROBLEM

An obvious condition that may be significantly related to the acquiring of perceptual prerequisites is the number of differential cues. As a first approximation to the much larger task of systematically varying the number of cues (relevant and irrelevant), this experiment has been designed to test the following hypothesis: Assuming that evidence of latent learning is found, this evidence will show that such learning is more effectively accomplished in that one of two similar situations which provides the larger number of differential cues.

A satisfactory test of the hypothesis requires detailed records of the *S*s' exploratory and test behavior. Such records will provide evidence concerning the possibility that cul entries are eliminated from maze runs by progressive reduction of depth of entrances. This has been the subject of much discussion and some experimental investigation (5).

The possibility that the elimination of culs is a consequence of the conditioning of an avoidance response to the "dead end" of a cul, the reinforcement being unimpeded movement along the through path, is so important that a second hypothesis has been submitted to experimental test, viz.: In the absence of any known incentive other than an open pathway, progressive reduction of depth of cul entries will not occur during periods of unguided exploration in a multiple-T maze which eliminates all visual cues from the culs and provides a pathway that is wide enough to allow the animals (rats) to turn around easily at any point.

METHOD

Briefly outlined, the plan of the experiment is: (*a*) to give equated groups of rats exploratory periods in two mazes that differ in the number of differential cues available, (*b*) to have the animals do the exploring while satiated for food and water, (*c*) to eliminate or otherwise control all known sources of differential reinforcement, (*d*) to make detailed records of the exploratory behavior and of the performances of the two groups on an experimentally motivated test trial, (*e*) to compare the test results of the experimental groups with results secured from a control group which was not given the opportunity to explore the mazes, and (*f*) to compare the effects of the two mazes upon the activities of the two experimental groups with special consideration of depth of entries into culs.

Apparatus

The floor plan and significant construction details of the two, five-unit T mazes are shown in Figure 1.

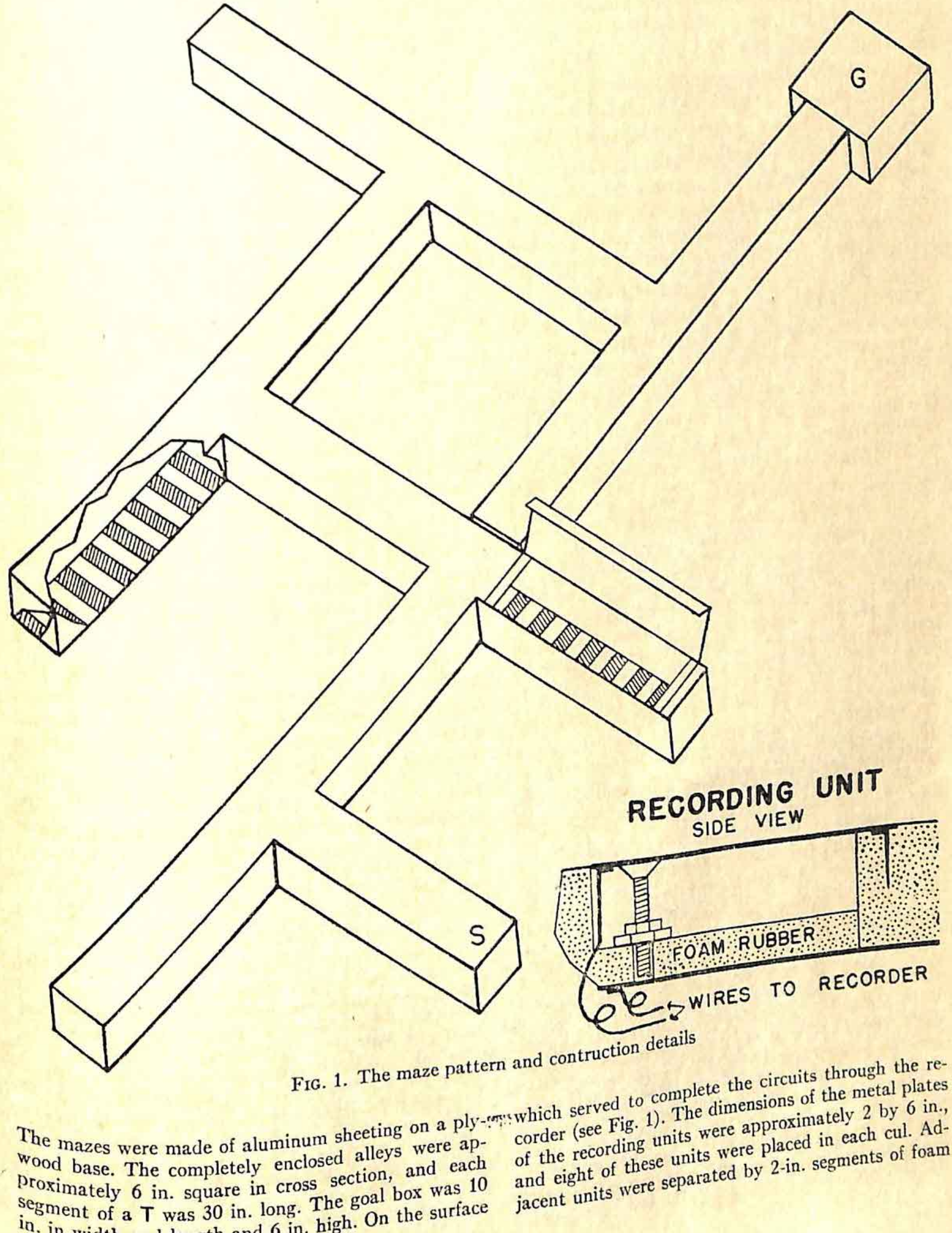

FIG. 1. The maze pattern and contruction details

The mazes were made of aluminum sheeting on a plywood base. The completely enclosed alleys were approximately 6 in. square in cross section, and each segment of a T was 30 in. long. The goal box was 10 in. in width and length and 6 in. high. On the surface of the plywood base of each alley a sheet of aluminum was placed with an attached wire leading from the metal plate to one terminal of an Esterline-Angus Multiple Recorder. Over the metal plates, a ¾-in. layer of foam rubber covered the entire base. Inserted into the rubber cushion were electrical recording units which served to complete the circuits through the recorder (see Fig. 1). The dimensions of the metal plates of the recording units were approximately 2 by 6 in., and eight of these units were placed in each cul. Adjacent units were separated by 2-in. segments of foam rubber. One unit was placed 2 in. past the entrance from the choice point in each of the open sections of the maze and in the goal box. The units were inaudible in operation; when depressed by the weight of an animal, they moved no more than other parts of the path; they could not shock the animals; and they operated reliably.

The running surface was a waterproofed fabric cover fastened securely on top of the foam rubber and the recording units. The consistency of the running surface was approximately uniform throughout the mazes. For half of each group of *S*s, the culs had a fine texture and the through pathway had a coarse texture. For the other half, the culs were coarse and the through path was fine. The fine texture was the natural texture of the fabric cover. A much coarser texture was provided by gluing 6-in. lengths of ⅛-in. twine coated with shellac across the width of the fabric cover at 1½-in. intervals.

The completely enclosed alleys excluded all light from one of the mazes (Maze *A*) and so eliminated all visual cues. Minimal, differential visual cues were supplied in the second maze (Maze *A*+) by inserting ¼-in. circular red light filters along the sides of the through pathways and in the goal box. These light cues were placed 8 in. apart 1½ in. above the running surface. The intensity of the light was kept constant, and, to the human eye, there was no illumination of the inner walls of the maze. These cues were merely distinctive red dots along the through path. The top of each segment of the mazes was hinged.

Subjects

The *S*s were 70 experimentally naive white rats 65 to 80 days old raised from birth in the Oberlin Animal Laboratory. These animals were housed in ¼-in. wire-mesh cages and had run on no surface other than that of the cage. They were distributed so as to equate groups for age, litter, and sex. The animals were run at a somewhat younger age than is customary because we expected them to be more active while satiated than older *S*s.

All animals were fed on the same standard diet, at the same time intervals, and were cared for by the same *E*s. All the animals were given approximately 5-min. daily, individual handling during the week before they were placed in a maze.

A surplus of food and water was always in the living cages at the time of each exploratory run, and an abundance of food and water had been in the usual containers for several hours before these trials.

Procedure

Two groups of five *S*s each were used to determine whether we should expect the main experimental groups to show an immediate preference for any of the four differentiating conditions. Each animal in one group was given 10 3-min. trials in a single, straight dark alley having a fine texture on one half the running surface and coarse on the other half. Each *S* in the other group was given its trials in a similar alley with one half having red dots, the other half completely dark, and with a fine texture on both halves of the running surface. All animals were placed in the alley at the mid-point, and evidence for a preference was secured by recording the amount of time spent in each half of the alley. The ten animals in these two groups were not used again in this experiment. The results for these preliminary groups caused us to counterbalance floor textures as described above.

In the main part of the experiment, each of 20 rats was given 20 periods of unrewarded exploration in Maze *A*, and *S*s in an equated group of 20 were given 20 unrewarded, exploratory periods in Maze *A*+. For both groups, the following controls, in addition to those previously discussed, were employed. (*a*) The animals had never secured food or water outside the home cages. Every aspect of the mazes was so different from the conditions of the home cages that secondary reinforcement mediated by stimulus generalization seems highly improbable. (*b*) The foam rubber was an efficient muffler of sounds within the mazes. Sounds produced by remote sources and by movements of the *E*s were so rare and variable that they could not constitute differential cues. The recorder was placed in an adjoining room. (*c*) Differential olfactory cues were avoided by removing feces and urine and by using an extra animal to "track" all parts of the running surface in a highly irregular way. (*d*) The place of entrance into the mazes was varied irregularly on successive exploratory trials, each animal being put into the first and second halves of the mazes equally often. (*e*) The *S*s were never removed from the goal box. (They did not remain in it long enough to make this necessary.) The place of removal varied greatly for each animal. Prodding the animals to avoid repeated removals from the same place was not necessary. (*f*) The time of the exploratory periods varied from 3 to 7 min. The sequence of different times was the same for all animals of both groups, but the periods were varied irregularly to avoid the conditioning of "escape" to a constant time interval. (*g*) The intervals between exploratory trials were the same for all animals: two daily trials about 90 min. apart. (*h*) The exploratory and test runs were not forced or guided by doors such as are used to prevent retracing. (*i*) The mazes and the home cages were placed in rooms separated by a storage room. (*j*) Opening the hinged tops of the alleys between trials provided adequate ventilation for the relatively short exploratory periods.

A continuous record was made of the course of a rat's exploration throughout each of 800 exploratory periods.

The final test runs were made 48 hr. after the twentieth exploratory period. During the 48-hr. interval, there was no water in the home cages, and the only food given was in the form of dry biscuits. After 12 hr. of water deprivation, each rat was taken to the maze it had explored and placed in the goal box which had been temporarily shut off from the rest of the maze. A glass bowl (very different from the suspended small tubes used to supply water in the home cages) in the center of the goal-box floor was filled with water. Each rat remained in the box 2 min. and then was returned to the home cage. (No animal in either group drank during this period.) Twenty-four hours after the start of water deprivation, the animals were put into the goal box again for 2 min. with the top closed and water present. (All animals drank at this time. The bowl was replenished to keep the water at a marked level for each animal.) After 36 hr. of deprivation, each rat was placed in the goal box with water, with the top open until the rat began to drink, at which time it was closed and the rat was given 1 min. more in the closed box. (The average time before the animals started to drink was almost identical for the two groups: 83.55 sec. and 83.50 sec.) Forty-eight hours after the last exploratory period, the rats were placed at the start of the appropriate maze and their behavior in the maze was recorded.

TABLE 1

Performance of the Two Groups on the Test Trial

MEASURE	GROUP*	M	σ_M	*t*
Cul entries				
Frequency	E	1.05	0.28	7.7†
	C	4.75	0.39	
Depth	E	6.1	1.87	5.2†
	C	21.8	2.34	
Time of run, in sec.	E	65.8	18.1	13.6†
	C	370.4	13.2	

* For each comparison, *N* is 40 in the experimental group, 20 in the control group.

† Significant beyond the .01 confidence level.

A 7-min. time limit was set for the test trial. All animals (including those in the control group) were assigned 7 min. as their running time if they did not enter the goal box before this limit was reached.

The control group was not given the exploratory trials, but in every other way, from birth to the end of the test trial, the treatment of this group was identical with that of the experimental groups. One-half the 20 control animals was tested on each of the two mazes.

RESULTS

Experimental vs. control groups. The data make possible five comparisons of the performances of these groups on the test trial. Three comparisons appear in Table 1: frequency of cul entries, depth of cul entries, and time of test run. All three are significant at the .01 confidence level.

A cul entry or an error was recorded when an animal depressed one or more of the eight recording units in each cul. An entrance by the animal's forepaws of about 1 in. was required to depress the first unit. The number of successive units depressed represents depth of entrance; each unit after the first indicating 4 in. of distance. The mean depth per animal presented here is the sum of all entries divided by the number of animals.

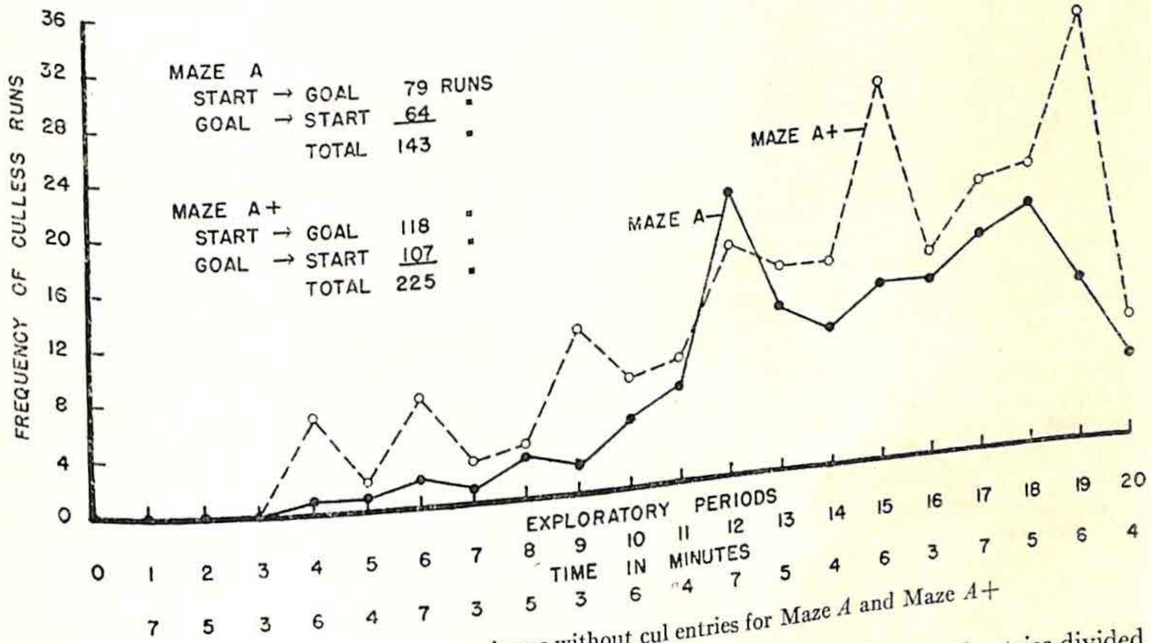

FIG. 2. Exploratory end-to-end runs without cul entries for Maze *A* and Maze *A+*

Two additional comparisons are not included in the table: The number of *S*s making errorless runs was zero for the control group and 23 (57.5 per cent) for the experimental group. The percentage of *S*s reaching the goal within 7 min. was 100 for the experimental group, 20 for the control group.

Maze A *vs. Maze* A+. An evaluation of the

TABLE 2
Frequency of Cul Entries during Exploration

MAZE*	PERIODS	M	σd	t
A	First 5	32.0	8.77	2.90†
	Last 5	37.8		
A+	First 5	30.2	7.55	5.78†
	Last 5	40.2		

* For each maze, *N* is 20.
† Significant beyond the .01 confidence level.

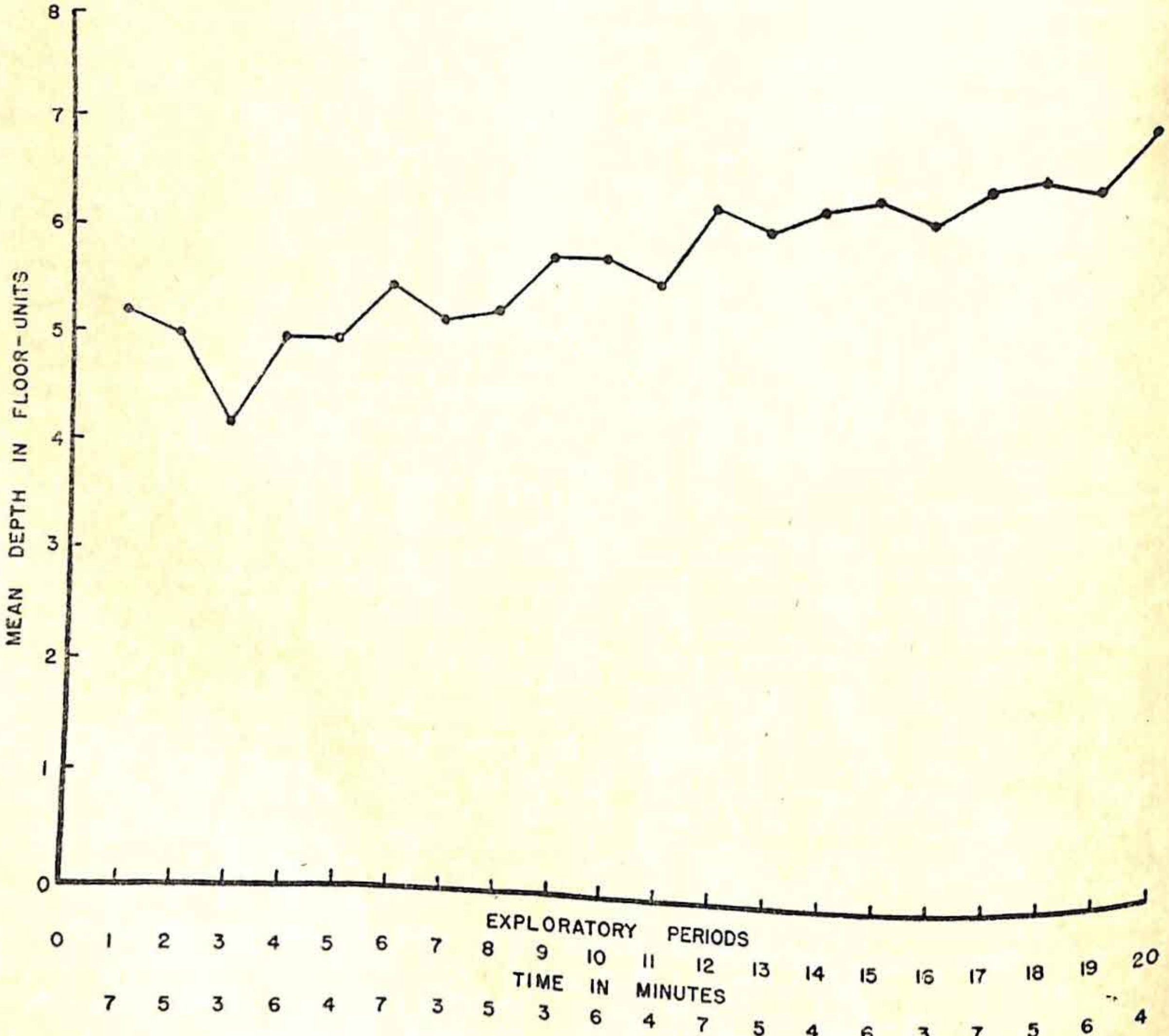

FIG. 3. Mean depth of cul entries during exploration of both mazes

relative effectiveness of the two mazes on the test trial requires three *t*-test comparisons. Frequency of cul entries for the two mazes was not significantly different ($p > .50$). Similarly, the two mazes did not differ in depth of entries ($p > .90$) or time of test run ($p > .70$).

End-to-end culless runs during exploration. After the third period of exploration, *S*s of both experimental groups began to make runs from either end of a maze to the other end without entering any cul. These runs of about 17 ft. were made in 15 to 25 sec. Only 3 of the 40 animals made all their culless runs in one direction, and these three made, together, only five such runs from the goal box to the start.

The end-to-end runs increased in frequency in successive periods but never consumed more than a small part of the total time of a period. Figure 2 shows this increase in frequency for Maze *A* and for Maze *A*+.

Maze *A*+ elicited significantly more ($t = 2.38$, $p < .05$) culless runs during the exploratory periods than Maze *A*.

Frequency of cul entries during exploration. The number of cul entries per minute increased during the exploratory periods. To test the significance of this increase, the combined results for the first five periods have been compared with the combined results for the last five periods (Table 2). Although the time of the exploratory periods was varied, the total time for the first five and for the last five periods was 25 min., and equivalent subdivisions of the total time were used. In making this comparison, the t test for related measures was used.

Depth of cul entries during exploration. As the frequency of cul entries increased, their mean depth increased in approximately equal amounts for the two mazes. The increase was significant at the .01 level, with $t = 6.8$. Figure 3 shows the mean depth of cul entries for the 40 experimental *S*s. The mean for each exploratory period, as shown in the figure, is based upon 150 or more cul entries. The largest number of entries in one period was 425.

TABLE 3

Exploratory "Errors" of Group 1 vs. Group 2

GROUP	N	M	σ_M	t	p
1	8	112	8.71	4.12	$<.01$
2	32	155	5.75		

Cul entries during exploration in relation to errors on test trials. The experimental *S*s have been divided into two groups: (1) those making 2 or more errors, and (2) those making less than 2 errors on the test trial. The group that made the smaller number of errors on the test made the larger number of cul entries during exploration (see Table 3).

Preference groups. We assumed that an immediate preference for any one of the four differential conditions (dark vs. red dots and fine vs. coarse texture) could be detected by means of the 100 records of 3-min. periods of unrestricted exploration. The 50 records for the dark- vs. red-dots condition show that the difference between the mean for each half of the alley and a mean of 90 sec. (representing equality) is 5.9 sec. This difference has a probability of .45, so a reliable preference is not indicated. The corresponding difference for the fine vs. coarse textures (37.1 sec.) has a probability of less than .01. A significant preference for the coarse texture is indicated.

Coarse vs. fine texture in relation to test performance. Although the preliminary preference group showed a reliable preference for the coarse texture, the test results of the experimental and control groups did not vary with texture of the maze. For frequency of cul entries, $p > .80$; for depth of cul entries, $p > .60$; for time from start to goal, $p > .20$.

DISCUSSION

The great superiority of the experimental over the control group is clearly shown by five different measurements of test performance. However, the pretest behavior of the experimental groups is known in some detail, and it includes end-to-end runs of the mazes without cul entries. Is there any justification, then, for the use of the term "latent" in connection with the pretest learning? An affirmative answer to this question must deal with essential aspects of the latent-learning problem.

Although *S*s of this experiment learned to discriminate the culs from the through path, it seems necessary to assume that a similar ability to discriminate between alternate response possibilities has been acquired whenever evidence of latent learning has been presented. The critical question is: Will an imposed goal elicit an appropriately discriminative performance? There seems to be no obvious reason why the behavioral changes involved in perceptual learning should be unobservable.

The causes and consequences of such learning may not be immediately apparent, and that seems clearly to be true in this experiment. First, before the test trial, no animal had made a culless run from start to goal immediately after it was placed in the maze. Entering the maze at different places restricted the possibilities of immediate end-to-end runs, but even when *S*s were placed at points near the goal or the start, they always entered some culs before starting a culless run. Second, the culless runs occurred in both directions (goal to start and start to goal) and in highly irregular sequences. These runs were episodes in a context of exploration that included repeated cul entries. That these reversible episodes would enable 57 per cent of the *S*s to make errorless test runs and an additional 22 per cent to avoid

4 of the 5 culs was only an unrealized possibility before the test. Third, although culless runs in both directions tended to increase in number on successive explorations, there was a parallel tendency for cul entries to increase in both depth and frequency. Under these circumstances, the immediate occurrence of a complex pattern of appropriately goal-directed behavior was certainly not manifest. Fourth, no direct or observable association of the responses at the five choice points and the thirst drive or the reinforcement of this drive had occurred before the test (3). Nevertheless, 48 hr. after the last exploratory period and 12 hr. after the second goal-box reinforcement, a highly significant number of errorless runs occurred.

The first hypothesis is supported only by the results for the exploratory periods. All animals in both experimental groups had made culless end-to-end runs during exploration, and although *S*s of Maze *A*+ made these runs more frequently, *S*s of Maze *A* were not inferior to them on the test.

During free exploration of a single T, *S*s undoubtedly run repeatedly over the segments which will later constitute the correct pathway (4, 8), as they did in this study, but, since spatially separate choice points are not available, evidence of learning is severely restricted, if not eliminated, by the experimental procedure.

The second hypothesis is supported with emphasis by the results. There was no decrease in cul exploration; indeed, there was an increase in both frequency and depth of cul entries.

Although there was an increase of both cul activities and culless runs in successive periods, during single exploratory periods the pattern or sequence of action shifted irregularly and often abruptly from successive cul entries to complete avoidance of culs and vice versa. Instead of a gradual reduction of cul activity, the results show an increasing frequency of completely accurate differentiations of cul activities and through-path activities.

The very great reduction and elimination of visual cues probably favored the increase in frequency and depth of cul entries during exploration. However, this limitation of visual cues could hardly be expected to favor errorless test runs unless increasing exploration of the culs enabled the animals to avoid them. The results do show that *S*s that were most successful on the test made the largest number of cul entries during exploration.

In addition to detailed recording of exploratory behavior in a multiple-T maze, the kinds of cues available to *S*s made some aspects of perceptual learning clearly apparent in this experiment. The floor textures could be explored only by movements of the whole body, whereas a visual texture can be explored over a relatively large area by less easily detected head and eye movements. Nevertheless, movements are involved in each case. It seems reasonable to assume that the floor textures of this experiment and the visual textures ordinarily available to rats in mazes differ more in complexity and in the kinds of movements they elicit than in their sign function in perceiving.

The results support the general conclusion that the minimizing of irrelevant or nondifferential features of the mazes and the addition of minimal, differential, visual cues have facilitated perceptual learning during unrewarded exploration. A decrease in depth and frequency of cul entries is not a necessary condition of such learning.

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NEED REDUCTION AND PRIMARY REINFORCEMENT:

MAZE LEARNING BY SODIUM-DEPRIVED RATS FOR A SUBTHRESHOLD SALINE REWARD[1]

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A central problem regarding the nature of reinforcement is whether it is to be identified with need reduction (4, p. 107). This identity is basic to Hull's (5) distinction between primary and secondary reinforcement, and it appears to be necessary if we are to escape the situation wherein we know a reinforcer solely by its capacity to reinforce. Yet the factual basis of the identity remains obscure.

"Primary reinforcement" is a term frequently met in the literature, but not always, or even usually, is it used strictly in accordance with the need-reduction hypothesis. To most authors the ingestion of food by a hungry rat is primary reinforcement. And normally, Hullian primary reinforcement does result. But by the need-reduction hypothesis, the stimulation from the food and its ingestion is secondary reinforcement which has acquired reinforcing properties by reason of its association with need reduction (5, p. 99). If this hypothesis is to conform to the facts, then the problem is to accumulate conforming facts: to show that tasting and ingesting food are not inherently reinforcing but that assimilating food is.

The solution of this problem demands that the stimulation from the food and its ingestion be dissociated from the natural physiologic consequences. To this end the esophageal-fistula experiment is often suggested (5, p. 99; 10, pp. 256–257; 17), but the experiment is so difficult technically that data from it are very slow to accumulate (6, 8, 9). An alternative method of dissociation was presented by Sheffield and Roby (15). They divorced need reduction from the direct stimulation of ingestion by using a nonnourishing, sweet-tasting saccharin solution as the incentive. Their results were, they believed, most easily explained by the assumption that the sweet taste was itself rewarding, that need reduction neither established nor supported the reinforcing character of the taste. That explanation is reasonable. If accepted, it means that at least some primary reinforcement is directly sensory. However, the experiment did not rule out entirely the possibility of need reduction as the fundamental basis of reinforcement, for even aside from pre-experimental experience of the animals, they were receiving food regularly, and at least once a day flavor stimuli (including sweet) as secondary rewards were receiving strong primary reinforcement. Further, although saccharin is nonnutritive, it is not entirely without physiological effect (2), albeit the effect can ill be termed need reduction.

The complement to the Sheffield and Roby approach is to make the animal insensitive (anesthetic) to the factor which reduces need and then to test whether need reduction unaided will generate secondary-reward value in stimuli only coincidentally associated with it. Some evidence along this line is already available from studies on food selection (3, 14, 19). These studies show that an animal may come to prefer some particular food if that food satisfies some particular need, but the skeptic may be left unconvinced that it is need reduction rather than flavor which is reinforcing. Our present purpose is to answer the skeptic: to show that need reduction per se can be reinforcing.

METHOD

Briefly, the experimental procedure was to make a group of ageusic and anosmic rats sodium deficient and then to train them on a single-unit T maze in which saline was the incentive. Normal animals were similarly trained as a control.

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[1] The data for this paper were gathered by C. W. T. and presented in different context (titled "Chemoreception, Learning, and Specific Hunger Behavior in the White Rat") in partial fulfillment of the requirements for the Ph.D. degree. P. B. P. is largely responsible for the present treatment.

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Subjects

The animals used were 21 Wistar albino rats reared locally. Eight of the rats were made sensory deficient and sodium deprived (Group E); 8 were sodium deprived only (Group A); and 5, nondeprived (Group B). Two rats of Group E were discarded from the tabulation of results because preference tests indicated them to be sensitive to weak saline. (Data justifying the discard of these animals are presented by Thomson [16, p. 75].) The rats were approximately 7 mo. old when those of Group E were made ageusic, 8 mo. old when these same animals were made anosmic, and 15 mo. old when all were trained.

Surgery

The operations to produce ageusia consisted of bilateral sectioning of the lingual (including the chorda tympani) and the glossopharyngeal nerves. The vagus was left intact. In order to minimize regenerative reinnervation and functional recovery, as much of the distal portions of the nerves as possible was pulled out. This operation greatly reduces but does not eliminate the rat's sensitivity to salt (11). In addition, because of the remote possibility that some of the residual sensitivity is olfactory (we are aware of no direct evidence either way), it was decided to attack olfaction also. This was done by severing the olfactory tracts with a cautery.

TABLE 1

Composition of Synthetic Diet

CONSTITUENT	PER CENT BY WEIGHT	CONSTITUENT	PER CENT BY WEIGHT
Casein ("vitamin free")	20.7	Sucrose	51.9
Corn oil (Mazola)	13.7	Cellu flour	8.7
Salts (sodium free)*	3.5	Vitamin B complex	1.4
Oleum Percomorphum (40 drops per kilo)			

* Parts by weight: KCl, 5.4; $MgSO_4$, 13.3; KH_2PO_4, 9.6; K_3PO_4, 23.4; $CaHPO_4$, 13.3; ferric citrate, 2.9; calcium lactate, 31.9.

At the termination of the experiment the operates were subjected to macroscopic post-mortem examination. Some regeneration of Nerve VII was evident in four of the six animals, and of Nerve IX, in three. Degeneration of the olfactory bulbs was complete in three animals and nearly so in the remaining three.

Diets

During most of the experiment the animals were fed the regular laboratory diet of Purina dog pellets ad lib., and Group B was so maintained throughout the experiment. Sodium deficiency was induced in Groups E and A by maintaining the animals on the sodium-low diet described by Table 1. The deficiency was induced on two occasions, each of which consisted of a 14-day depletion period plus, in the first instance, 24 days of preference tests, and in the second instance, the period of maze training. The periods of deprivation were separated by 14 days on the regular laboratory diet.

PREFERENCE TESTING

In order to determine the effectiveness of the sensory deprivations on Group E, Groups E and A were subjected to preference tests for saline. The tests were run twice, first under conditions of normal laboratory maintenance, then under conditions of sodium deprivation.

Method

The rats, individually caged, were each presented with two Richter-type drinking tubes. One tube contained saline, the other, distilled water. The salt concentration in the saline tube was increased every 48 hr., as indicated along the abscissa of Figure 1. To control possible tube and position preferences, the locations of the saline and the water were alternated every 24 hr.; i.e., the drinking tubes were not moved but the contents were. A preference threshold was taken to be indicated when the animals drank significantly more of one fluid than of the other.

After completion of the first test series, the animals were continued on the regular colony regimen for seven days. Then sodium deprivation was begun, and after a 14-day depletion period a second test series was run in the same manner as the first.

Results

The mean quantities of saline and water ingested during the preference tests are shown in Figures 1 and 2. Before deprivation for sodium the Group A animals exhibited a preference for saline similar to that found by other investigators (e.g., 1, 18). Under conditions of sodium deprivation these same animals showed an exaggerated preference for saline, the threshold being below the lowest concentration of salt (0.01 per cent) tested—again a value similar to that found by others (1, 13) for sodium-deficient (adrenalectomized) rats.

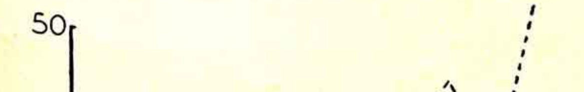
Group E showed no preference for saline of concentrations less than 0.4 per cent salt. At approximately this concentration, under both the normal and the sodium-low dietary, these animals began to show a preference which became more pronounced at the higher concentrations.

INITIAL DISCRIMINATION TRAINING

From the evidence collected in the preference tests a concentration of salt which was superthreshold to the normal rats but subthreshold to the sensory deficient was selected. This concentration (0.1 per cent) was then used as the incentive in a single-unit T maze. The problem set the animals was a simple right-left discrimination.

Method

In this phase of the experiment all three groups of animals were used—Group E (sensory deficient and sodium deprived), Group A (sodium deprived), and Group B (nondeprived). Groups E and A were, after the preference tests and 14 days on the regular laboratory diet, redepleted for sodium by being maintained on the sodium-low diet (Table 1) for 14 days prior to maze training. Group B was fed the Purina pellets. These regimens were now continued throughout the training period.



* Preference threshold for saline for the control group (*A*). The difference between saline and water intakes reached statistical significance ($t = 2.38$, 8 *df*) at this concentration.

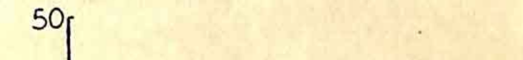
† Preference threshold for saline for the sensory-deficient group (*E*). Statistical significance ($t = 3.86$, 6 *df*) first appeared at this concentration, was lost at the next higher concentration ($t = 0.96$), and reappeared thereafter (t's > 3).

FIG. 1. Mean quantities of fluid ingested by the rats when not deprived of sodium. (Each point represents the quantity drunk in 48 hr. Concentrations greater than zero are spaced on a log scale.)

The maze was an alley T, the stem and each arm of which were 20 in. long. Guillotine-type doors were at the start box, at the central end of each arm, and at each goal box. The doors in the arms of the T were used to block one or the other arm so as to permit the rat no choice of goal box on the "forced" trials. The goal-box doors barred the rat from leaving a goal box once entered. A Richter tube in the "correct" goal box contained saline, in the other, distilled water. For half the rats the left goal box was correct, for the others, the right.

During the four days immediately preceding maze training, the animals were adapted to the maze situation (minus the drinking tubes) by being allowed individually to explore the maze for 15 min. each day.

For the first days of maze training each animal was motivated to drink by being deprived of water 12 hr. (From 9:00 A.M. to 9:00 P.M. All training sessions began at 9.00 P.M.) On these days the rats were forced to the right and left goal boxes alternately, four trials each day, until each animal had drunk three times in each goal box. For most rats this training was accomplished in two days, and for all, in three. On each trial the rat was confined in the goal box for 3 min. or until it drank. If the animal drank, it was immediately removed from the goal box and placed in a holding cage until the next trial. This training was designed to teach the animals to run the maze and to drink. Differential running to water and to saline might have been set up but could hardly have been exhibited.



* Significant preference for saline shown by the control group at this and all subsequent concentrations (t's > 2.7, 8 *df*).

† Preference threshold for saline for the sensory-deficient group. Statistical significance is indicated by $t = 4.61$, 6 *df*. The t's from lesser concentrations were all less than 2.

FIG. 2. Mean quantities of fluid ingested by the rats when on the synthetic, sodium-low diet (curves are to be read as in Fig. 1)

Following these forced trials run under the motivation of water deprivation, the animals were given 10 days of discrimination training. On these days they were not deprived of water, the only special motivating condition being the sodium need. They were free to choose either arm of the maze, but not to reverse a choice once made. Four trials, about 15 min. apart, were given each day. Occasionally a rat would delay leaving the start box for as long as 3 min. When this occurred the rat was removed from the maze and the trial recorded as "no choice." (Out of 720 trials [40 per rat], 62 were "no choice." The distribution of these trials was: Group E—24 trials, by 2 rats; Group A—16 trials, by 3 rats; Group B—22 trials, by 2 rats.) On each "choice" trial the rat was confined in the goal box for 2 min. or until it drank. Drinking was in each instance limited to a couple of laps so that the sodium deficiencies would not be overcome by the ingestion of saline.

Results

The percentages of correct choices are summarized in Figure 3. Groups E and B never deviated significantly from chance (50 per cent correct) in their choices, nor did any individual animal. Group A animals improved in percentage of correct responses fairly consistently. By the end of training, all of this group had learned to choose the arm which held the saline; no rat made more than one error per day on any of the last three days.

On reaching the goal box an animal might or might not drink. Figure 4 shows the percentage of opportunities to drink which resulted in drinking. For the first seven days, the experimentals (Group E) drank about half the time and with approximately equal frequency in each goal box. On the three following days, correct choices were followed by drinking approximately 90 per cent of the time, whereas incorrect choices were followed by drinking 50 per cent of the time as before.

The chi squares, corrected for continuity, relating to this differential drinking on days 8 to 10 were, for the individual rats: 0, .4, 0, .04, 4.3, and 6.3, 1 *df*. The two rats which seem here to be discriminating are those considered below in step *e* of the modified discrimination training. Discrimination by the Group A rats is obvious. The Group B rats (not represented in Fig. 4) drank on about half their trials and indiscriminately in the two goal boxes.

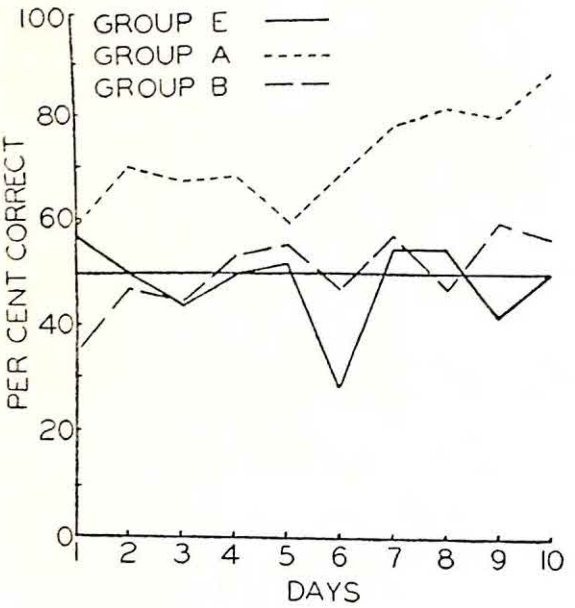


FIG. 3. Percentage of choices made to the correct (saline) side of the maze

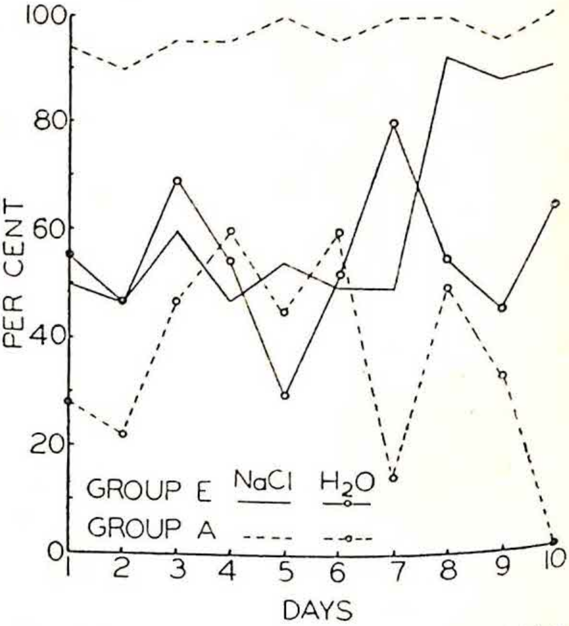


FIG. 4. Percentage of choices followed by drinking in the chosen goal box

MODIFIED DISCRIMINATION TRAINING

During the initial training period the Group A rats learned the location of the saline, indicating that the problem was readily learnable and that the sodium deprivation provided a sufficient motive. The Group E animals failed, and it was decided to modify the training procedure for them as might prove necessary to overcome that failure.

Method

The modified training procedure included the following sequence of events:

a. Four days of alternating free and forced runs, four per day, under 12 hr. of water deprivation. The forced runs were to the side not taken on the free trials.

b. Two days, four trials per day, on which all trials were free choice. On these days the rats were not deprived of water.

c. Two days, without water deprivation, on which all four trials each day were forced to the correct (salt incentive) side.

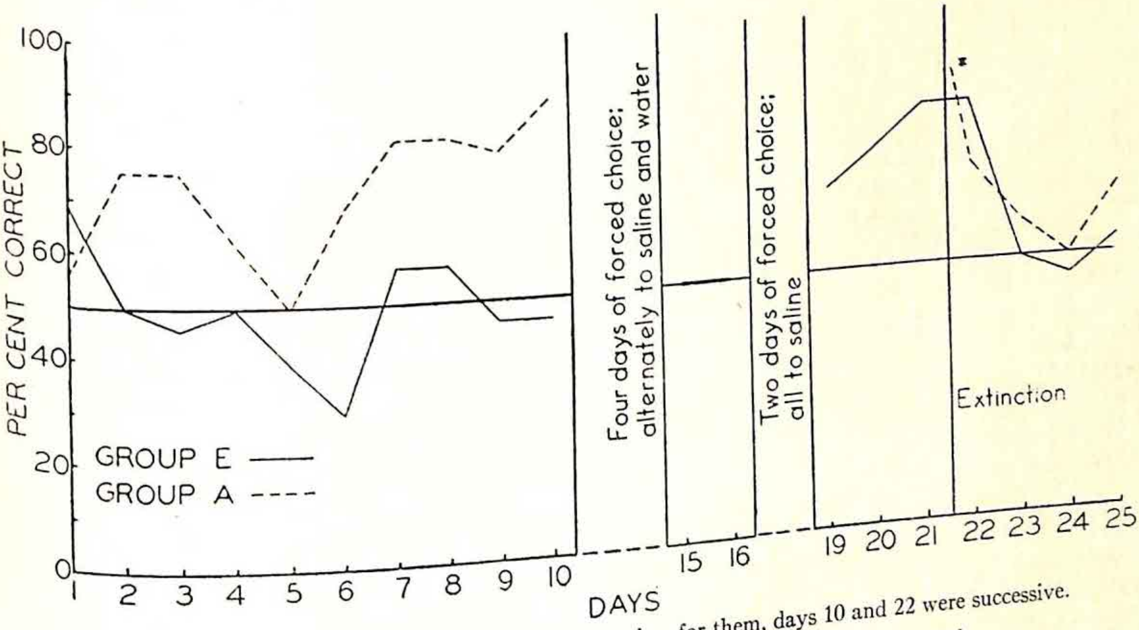
d. Three days of free-choice runs, four per day, without water deprivation.

e. For two rats still choosing at the 50 per cent level, steps *a* and *d* were repeated with the incentive solution of salt raised to superthreshold strength (0.8 per cent).

f. For the four experimental rats not included in step *e* and for four Group A rats, extinction trials were run with distilled water in both goal boxes. This training was continued until the preference for the formerly rewarded goal was no longer shown.

Results

Step *a* resulted in regular drinking by all animals on all trials, thereby again permitting the correct and incorrect arms of the maze to be associated with the saline and water, respectively. On the free choices of step *b*, exactly 50 per cent of the choices each day were correct. No discrimination was indicated.



* This point corresponds to day 10 for the Group A rats; i.e., for them, days 10 and 22 were successive. extinction trials

FIG. 5. Percentage of correct choices made by those rats given extinction trials

During the three days of step *d*, four rats came to choose the correct side progressively more often (days 19 to 21, Fig. 5). The chi squares, corrected for continuity, relating to these scores of these four rats were: 1.5, 2.1, 2.1, and 1.5, 1 *df*. Or, as there was no significant interaction, the corrected chi square for all trials of all four rats was 9.6, 1 *df*. Time scores improved correspondingly.

Figure 5 is a comparison of the choices of the rats trained on step *f*. The pre-extinction performance is shown also. In extinction, the performance of the Group A animals deteriorated on the first day, whereas that of Group E did not. The difference between the mean changes in percentage of correct responses was reliable, as indicated by a *t* of 3.27, 6 *df*. Furthermore, there was a qualitative difference in the animals' reactions to the distilled water in the formerly correct goal. On the first trial the control rats started to drink as usual but immediately left off, turned around, and tried to leave the goal box. On the second trial they again seemed to take a quick sip but then attacked the drinking tube by biting and tried in every way to force their way out of the goal box. The experimental rats, on the other hand, ran and drank just as on the previous days. On the second extinction day, their performance, both in time and errors, deteriorated, but at no time did they appear frustrated at finding distilled water.

The two Group E rats which showed no improvement during step *d* promptly came to choose correctly during step *e*.

DISCUSSION

Whether these results are accepted as relevant to our problem depends directly on our success in reducing the salt sensitivity of the Group E rats below the incentive concentration. The statistical nature of thresholds makes this difficult of demonstration, but the difficulty may be met by a review of the pertinent data. First, there is the failure of these rats to discriminate in favor of the incentive concentration of saline during the preference tests. The Group A rats exhibited a preference threshold of about the value reported by Pfaffmann and Bare (11) as the probable absolute threshold. This suggests that when receiving a sodium-deficient diet, as when adrenalectomized, the rat's preference threshold may be taken as an approximation of its absolute threshold. Inasmuch as the Group E animals were ingesting, during the preference tests, even less saline than those of Group A, their need for sodium must have been at least as great. This need would be somewhat alleviated by the salt taken in through the indiscriminate ingestion of saline and distilled water, especially as the concentrations of salt became greater; but accepting McCoy's statement of the rat's sodium requirement (7, p. 98), one finds the need would not have been overcome at any concentration below 0.4 per cent. It is, presumably, a coincidence that this concentration also marked the preference threshold. Second, the behavior of the four Group E animals given extinction training was hardly consonant with the hypothesis that these animals could distinguish between the incentive saline and the substituted distilled water.

Also relevant to our problem is whether the preferences shown by the Group E rats reflect learning related to the ingested saline rather than to some other factor. The first question here is of the adequacy of the evidence that four rats of Group E learned the maze during step *d* of the modified training. Although the chi squares are low, several factors support the judgment that learning occurred. The improvement in performance following the forced trials of step *c* was progressive; it seems not to have been a simple continuation of the forced-trial behavior. Further, psychological literature no place reveals that forced trials, usually called guidance, are very effective in producing the stereotypy characteristic of the maze habit. It is also noteworthy that the preference for the correct alley deteriorated as soon as the saline was replaced with water; it apparently depended upon the saline reinforcement. And finally, the training procedures followed appear peculiarly unsuited to the development of position habits unsupported by reinforcement; no rat of any group chose the water side of the maze on all four trials of any day or even on three trials of the four for more than two days consecutively. Thus, it appears that at no time were the rats choosing randomly; rather they were exhibiting throughout training either a saline preference or an alternation preference.

If we grant that the saline was in fact subthreshold but yet the rats ran the maze for it, it follows that need reduction can support learning—that under certain conditions, at least, primary reinforcement is identical with need reduction. This is not the complete proof of Hull's identity hypothesis, but a step; still to be shown is whether no class of stimulation is reinforcing antecedent to its association with need reduction.

Although our data support one aspect of Hullian theory, they appear critical of another. This is the gradient of reinforcement. Hull (5, p. 142) supposed that for rats the gradient of reinforcement is limited in time to something less than 30 sec. In our situation this interval must be far too short. Fifteen minutes was the interval between trials, but apparently it was not long enough for need reduction (reinforcement) to occur. During the training period when choices were first to one then to the other goal, neither choice was resulting in need reduction, although both together were. Later, when all choices were forced to the correct side, the need reduction consequent to the ingestion of saline could be unequivocally associated with that goal box and learning occurred. This interpretation is not controverted by the possibility that two of the Group E rats may have learned to discriminate saline during the first training series; one need but suppose that for them a sufficient degree of need reduction occurred between trials whereas for the others this degree was reached only between days.

SUMMARY

Six ageusic and anosmic rats were made sodium deficient and then trained on a single-

unit T maze in which subthreshold saline was the incentive. Eight normal animals were similarly treated and trained, as were five normals not made sodium deficient. The sensory-deficient rats failed to learn the maze until the training procedure was modified so that for two days all trials were forced to the saline side or until the concentration of the saline was raised to a superthreshold value.

Learning to choose the goal box containing subthreshold saline is taken to indicate that need reduction can serve as reinforcement independent of direct sensory "reward." To establish that need reduction can so serve is a necessary step in substantiating Hull's hypothesis of identity between need reduction and primary reinforcement.

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QUANTITY OF FOOD INGESTED AS A MEASURE OF RELATIVE ACCEPTABILITY

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In a previous experiment (7) it was found that two methods of testing preference gave different results. With one method rats were housed in individual testing cages and given a 24-hr. continuous choice between two fluids—distilled water and a sugar solution. The relative quantities of fluid accepted per day indicated a peak concentration, or optimum, at about 8.5 per cent. The existence of an optimal concentration confirms a previous finding of Richter and Campbell (5). With another method of testing, the two fluids were exposed briefly for choice on the preference apparatus. With this brief-exposure preference method it was found that a 50-per cent sugar solution was preferred to a 4-per cent solution and that both of these were preferred to distilled water. In other words, the higher the concentration, the greater the acceptability, no optimal concentration being apparent. Since completion of the present experiment, Stellar and McCleary (6), relying upon the quantity of food accepted as a measure of relative acceptability, reported that relative acceptability varies with the method of testing preference.

The present work was undertaken to explain why different methods of testing preference yield different results. The conditions of maintenance and pretest deprivation employed in the former experiment were modified so that a better comparison of methods could be made.

METHOD

To eliminate the possibility that bodily need is a factor in the results, rats used as *S*s in the present work were housed in group cages containing an unlimited supply of Purina rodent cubes and tap water. The animals were removed from maintenance cages at the start of every preference test and returned immediately after completion of the test.

The brief-exposure technique and preference apparatus have been described elsewhere (8). In this technique rats are trained to shuttle between a starting box and a pair of test foods. When one food is accepted, both are lowered from reach of the animal. The choice is recorded.

The apparatus employed in tests with continuous exposure of fluids has been described in a previous paper (9). The front of the apparatus is designed so that from 1 to 5 Lucite blocks, each containing a 1-in. drinking cup, can be inserted in the cage. Each block supports a glass tube partly filled with test fluid. Block, tube, and contents can be weighed on an ordinary balance with a precision of 0.1 gm. The tube contains a float and filament for continuously recording the rate of acceptance.

All tests of relative acceptability were made with sugar (sucrose) solutions. We selected, for special study, concentrations of 9, 18, and 36 per cent. Supplementary tests were made with distilled water (0.0), with a 60-per cent sucrose solution, and with crystalline sucrose (S). The percentage concentrations in the present work are all by weight of solute and solvent, e.g., a 9-per cent solution contains 9 gm. of sucrose and 91 gm. of distilled water in 100 gm. of solution.

RESULTS

Tests with the Brief-Exposure Preference Method

Six rats, three of each sex, were given a series of preference tests with the brief-exposure method. Each rat was given a series of 100 choices between sucrose solutions: (*a*) at 36 and 18 per cent, (*b*) at 36 and 9 per cent, (*c*) at 18 and 9 per cent. The order of taking the tests was rotated so that two of the rats commenced with the first combination of solutions, two with the second, and two with the third. No solution, therefore, had any consistent advantage of priority.

In scoring the tests, a pair of successive choices, with the foods in the AB and BA positions, was rated as a unit. Each pair of successive choices was counted as showing: (*a*) a preference for the higher concentration, or (*b*) no preference (=), or (*c*) a preference for the lower concentration. Twenty successive choices (ten pairs) constituted a test in the tabulation of results.

Table 1 is a summary of the total findings for the group of six rats. The results have been fractionated to show the preference in successive tests each summarizing 120 choices (60 pairs). A grand total of 1800 choices (900 pairs), equally distributed among the three pairs of test fluids, is summarized in Table 1.

The table shows a well-marked preference for the sucrose solution having the higher concentration, i.e., the sweeter solution. The raw data indicate that all six rats are consistent and uniform in their preference for the higher concentration. The five successive tests reveal a marked preferential trend. The preferred concentration becomes increasingly preferred with continued practice; the nonpreferred concentration becomes less and less frequently preferred with practice. The grand totals leave no room for doubt about the result.

The first preference tests, therefore, demonstrate clearly that the higher the concentration of sucrose solution, the higher the level of acceptability.

TABLE 1

Results of Preference Tests with Three Concentrations of Sucrose

TEST NUMBER	SUCROSE CONCENTRATION								
	36	=	18	36	=	9	18	=	9
1	9	36	15	34	19	7	21	28	11
2	13	36	11	35	21	4	27	28	5
3	24	26	10	37	23	0	30	27	3
4	26	31	3	45	15	0	34	24	2
5	29	27	4	42	17	1	34	25	1
Total	101	156	43	193	95	12	146	132	22

After obtaining the results summarized in Table 1, we wished to extend the series of concentrations above and below those originally presented in order to discover how far the above stated principle held true. First, we ran a test between a 9-per cent sucrose solution and distilled water (0.0). The results for the group of six animals are summarized at the left in Table 2. Pairs of successive choices were scored and tabulated by successive groups of ten runs (five pairs) per rat. Table 2 should be read like Table 1. The result of the series of tests is decisive. All rats showed a marked and increasing preference of 9-per cent sucrose solution over distilled water (0.0). The rapidly decreasing frequency of indifference (=) suggests that these two fluids are widely separated in acceptability when compared with the fluids shown in Table 1.

Next, a test of 80 choices (40 pairs) per rat was run between the 36- and the 60-per cent solutions. The 60-per cent concentration was chosen as one near to saturation. Results for the total group are summarized in the central columns of Table 2. Here it is clear that the 60-per cent solution is consistently and increasingly preferred to the 36-per cent solution. The range of indifference (=) is relatively large and the preference not as decisive as with the 9 and 0.0 fluids.

Finally, we ran a test of 50 choices (25 pairs) per rat with the 36-per cent solution and crystalline sucrose (S). The results are summarized at the right in Table 2. The 36-per cent solution was consistently and increasingly preferred to the sugar crystals by all rats in every test. In a control study with four naive rats, three preferred 36 per cent to S, and one preferred S to 36. Just where the acceptability of S would lie in relation to solutions of concentration lower than 36 remains to be determined. The result with S makes it clear that solid sugar is an exception to the generalization that the level of acceptability increases with concentration. The probable explanation lies in differences of physical state, texture, and appearance. Relative to the result with S, it is obvious that S is not a solution. Hence, for the present, we will disregard the tests with S and limit consideration to solutions.

In the first tests three concentrations of sucrose (9, 18, 36) had been tested systematically. The general plan was a modified method of paired comparisons. On the basis of Thorndike's computing procedure, cited by Guilford (3), we computed scale values for these three sugar solutions. Then we extended the scale to zero per cent (distilled water) and to 60 per cent (near saturation) on the basis of the percentages obtained in tests shown in Table 2. The computed scale values were as follows: 0.0 per cent, 0.000; 9 per cent, 1.183; 18 per cent, 1.720; 36 per cent, 1.963; and 60 per cent, 2.346.

When the computed scale values were

plotted against the logarithm of the concentration, the points departed but slightly from a straight line. In other words, there appears to be a linear relation between the level of acceptability, as tested, and the log of the concentration. It is probably correct to assume that the sweeter the taste the more acceptable it is.

Discussion. Results of preference tests agree with our previous findings with rats (7) and with the results of Engel (2) obtained with ten human *S*s. Engel instructed his *S*s to take about 10 cc. of sugar solution into the mouth for 20 to 30 sec. and then to report "acceptable," "indifferent," or "unacceptable." During six experimental sessions he obtained 56 reports for each of 11 concentrations. The graphic presentation of his results demonstrates that the frequency of the report "acceptable" increases with concentration from 1 to 9 per cent; above 9 per cent there is a ceiling and no decrease. Engel failed to find a peak, or optimum, at 9 or any other per cent. Moreover, four *S*s reported "very acceptable"; the frequency of this category of report increased steadily with concentration from 9- to 40-per cent (the highest) concentration.

TABLE 2

Preference Tests with Sucrose Solutions, Distilled Water, and Crystalline Sucrose

TEST NUMBER	TEST FOODS								
	9	=	0.0	60	=	36	36	=	S
1	18	12	0	5	48	7	18	8	4
2	28	2	0	11	49	0	24	5	1
3	29	1	0	32	27	1	23	7	0
4	30	0	0	33	27	0	30	0	0
5	29	1	0				26	4	0
Total	134	16	0	81	151	8	121	24	5

Engel's human *S*s and our rats (in two experiments) thus agree that the higher the concentration of sugar solution the more acceptable it is.

Acceptance Tests with the Single-Stimulus Method

Ten rats were tested simultaneously in individual cages for exactly 1 hr. Each cage contained a single sucrose solution presented in a container designed for graphic recording of acceptance during any continuous exposure. For each animal we obtained: (*a*) the intake, i.e., the total number of grams of fluid consumed during a 1-hr. period, and (*b*) the cumulative curve of acceptance.

Each rat was given a series of 12 daily 1-hr. tests for each of three solutions. Five *S*s took the tests in an ascending order of concentration: 9, 18, 36 per cent, and five took the tests in a descending order: 36, 18, 9 per cent. Tests were made on weekdays only.

Table 3 is a summary of the quantitative data for the group. For each rat individually[1] as well as for the group, the higher the concentration, the lower is the total intake of fluid during a 1-hr. drinking period. If the quantity of fluid accepted is a true measure of acceptability, then the 9-per cent solution is definitely more acceptable than 18, and the 18 is more acceptable than 36.

Figure 1 is based upon measurements of the acceptance curves during a series of 1-hr. tests. The upper curve is based upon measurements of 60 graphs (five rats, 12 days) with a 9-per cent sucrose solution. The lower curve is based upon measurements of 60 graphs (five other rats but the same 12 days) with a 36-per cent sucrose solution. Measurements of the graphs were made at 10-min. intervals throughout the hour, and each point in the figure is an average based on 60 measurements. The figure clearly demonstrates that the rate of accepting the 9-per cent solution is consistently higher than the rate of accepting the 36-per cent solution at all times during the 1-hr. test.

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[1] Individual data showing the range of fluid intake and average fluid intake for each concentration have been deposited with the American Documentation Institute and may be obtained by ordering Document 4019 from the ADI Auxiliary Publications Project, Photoduplication Service, % Library of Congress, Washington 25, D. C., remitting $1.25 for microfilm or $1.25 for photoprints.

Table 4 presents, at the left, the total number of grams of fluid consumed in all 12 tests by 9 rats. To make a fair comparison, the data for one rat, that died before completing the last test, were deleted. From these totals we have computed the number of grams of sucrose and the number of grams of water received from each solution. Table 4 shows that although the rats took less of the 36-per cent solution than of the 18 and the 9, they actually obtained considerably *more* sucrose from the concentrated solution. In fact, the higher the concentration, the more sucrose (relatively) and the less water (relatively) they ingested. The result is definitely out of line with a conclusion drawn by Hausmann (4) that the absolute amount of sugar absorbed is essentially independent of the concentration. Unfortunately, the data that Hausmann selected for publication do not adequately support his own conclusion. It is clear that the quantity of sucrose and of water ingested is a function of the concentration.

TABLE 3

Intake of Single Sucrose Solutions, in Grams of Fluid, during 1-Hr. Drinking Test

CONCENTRATION (per cent)	AV. FLUID INTAKE (gm.)	*SD* (gm.)
9	17.0	3.48
18	13.8	1.84
36	11.34*	1.31*

* Based on data from nine *Ss*. Other averages and *SD*'s are based on data from ten *Ss*.

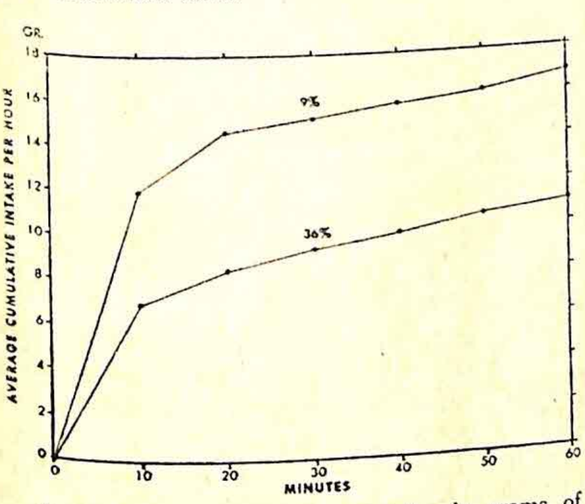

FIG. 1. Average cumulative intake, in grams of fluid, of two sucrose solutions presented singly for 1 hr.

Discussion. If the *quantity of food accepted* (grams per hour) measures acceptability, then the 9-per cent solution must be regarded as more highly acceptable than the 36. If the *rate of acceptance*, as recorded in the graphs, is a measure of relative acceptability, again, the 9-per cent solution must be regarded as more acceptable than the 36 at all stages during the 1-hr. test.

This greater acceptability of sugar solutions at a concentration of 9 per cent agrees with the findings in other studies in which the quantity of food accepted per day has been taken as a measure of acceptability. As mentioned above, Richter and Campbell (5), in preference tests between distilled water and several different kinds of sugars, found a peak of high acceptability at about 8 per cent; and Young (7) placed the peak of acceptability for sucrose at 8.5 per cent. These two experiments have in common the feature that sugar solutions were never paired with each other but always one sugar solution was paired with water.

TABLE 4

Amount of Sucrose and Water Consumed (grams)

% CONSUMED	TOTAL SOLUTION CONSUMED	GRAMS SUCROSE CONSUMED	GRAMS WATER CONSUMED
9	1530	137.7	1392.3
18	1236	222.5	1013.5
36	1021	367.6	653.4

At the close of the single-stimulus tests we predicted that the 9-per cent solution would be preferred to the 36-per cent in a 1-hr. preference test, but this prediction turned out to be incorrect.

Preference Tests with a 1-Hr. Exposure

Following the 1-hr. tests with single stimuli, the rats were given a similar preference test in the same cages. Each cage was provided with two Lucite-block cups, one containing a 9-per cent sucrose solution and the other a 36-per cent solution. The cups were symmetrically placed in the second and fourth of the five positions in the testing cages. Relative positions of the cups were interchanged from day to day as a control upon possible position habits. Each rat had exactly 1 hr. in the testing cage with a free choice between the two sucrose solutions. Intake in grams of fluid was determined as before by an initial and final weighing.

The total number of grams of fluid ingested during the hour is shown for each fluid in Table 5. For the experimental group each figure is an average based upon sixty 1-hr. preference tests. The individual data[2] indicate that of the 60 tests, 54 showed a greater acceptance of the 36-per cent solution than of the 9-per cent solution. Of the 6 exceptional results, 5 were obtained from a single animal. In general, there was a very marked preference for the 36-per cent solution, as shown by relative quantities accepted.

TABLE 5

Intake of Two Sucrose Solutions, in Grams of Fluid, during 1-Hr. Preference Test

GROUP	CONCENTRATION (per cent)	AV. FLUID INTAKE (gm.)	*SD* (gm.)
Experimental	9	2.97	2.42
	36	9.74	2.65
Control	9	3.49	1.21
	36	8.10	2.60

It is instructive to compare the intake of these fluids (Table 5) with the intake of the same fluids when presented singly (Table 3). Nine of the ten rats were *S*s in both tests. The rats took slightly less 36-per cent solution in the preference test than in the test with single stimuli, but in both tests the average intake was in the same range. With the 9-per cent solution, however, there was a marked drop in intake. The animals took from 2.3 to 20.6 times as much 9-per cent fluid when it was presented singly (without choice) as when it was presented along with the 36-per cent solution (with choice). The single deviant *S* took 2.5 times as much 9-per cent solution in the single-stimulus situation as in the two-stimulus situation.

Figure 2 shows the average intake of the two sugar solutions during six successive tests. The curves reveal the consistency of preference for the 36-per cent solution. The differences in intake for the six tests are all significant at better than the 1.0-per cent level of confidence, using a sign test.

We thought that this decisive result might in some way depend upon the experience of the rats. The rats had been given preference tests with these fluids with the brief-exposure method, and they had also experienced the test fluids repeatedly during work with single stimuli. Did previous experience with the test fluids in part determine the result?

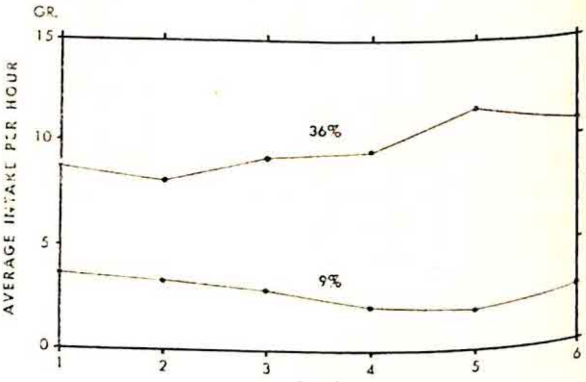

FIG. 2. Average intake per hour, in grams of fluid, of sucrose solutions during six successive preference tests

To answer this question ten naive rats were given the same preference test on four successive days. The naive animals were of the same age as the experimental rats, and they had had the same dietary history. Although the controls had been used as *S*s in tests with saccharine solutions, they had never experienced sugar solutions in any form prior to the present work.

Table 5 gives the average intake in grams of fluid for the control group in a series of four preference tests. Without exception the control rats took more grams of the 36-per cent solution than of the 9-per cent. There were, however, several unexplained reversals of preference on the last test. The significance of the difference was computed for the control rats. A sign test of the data showed a difference significant at the 1.0-per cent level. We conclude, therefore, that previous experience with sugar solutions was not a decisive factor determining the preference shown by rats in the experimental group.

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[2] Individual data are available in the tables deposited with ADI and may be obtained by ordering Document 4019 from ADI. See footnote 1 for details.

DISCUSSION

Beebe-Center and others (1) have demonstrated that the per diem intake of a fluid, presented in a single container, varies with the concentration of saccharine. They have suggested that since the single-stimulus method does not involve discrimination and differential "reinforcement," this method might be used in studying preference. The present results, however, indicate clearly that the single-stimulus method does not give a correct basis for prediction of preference. On the basis of results summarized in Table 3 we should predict a consistent preference of the 9- to 36-per cent sugar solution, contrary to the actual preference demonstrated by results in Table 5 and contrary to results with the brief-exposure method summarized in Table 1.

Preference implies the possibility of choice. Consequently, when there is only one stimulus fluid, there is no possibility of showing a true preference. All the techniques employed in the present investigation are methods for studying *relative acceptability* of test foods; but the relative acceptability as revealed by the single-stimulus method is different from the relative acceptability as revealed by methods that involve choice.

How can the discrepancy of results be explained? In answering this question, let us consider first what it is that the intake per hour or per day actually reveals. When a rat has unlimited access to a single fluid, he ingests it up to the limit of satiation. The intake per hour or per day measures a quantity of fluid required to satiate an animal or to keep it satiated throughout the exposure period. This quantity clearly varies with the characteristics of the test fluid as illustrated by Figure 1 and Table 3. The approach to satiation depends upon organic conditions that change with continued ingestion. With the present solutions both the solute and the solvent are involved in the approach to satiation. How the sucrose and the water factors are interrelated in the approach to satiation is a matter demanding further study (see Table 4).

The next point in the explanation of our results is that the sweeter solutions are more palatable than the less sweet. Results of preference tests summarized in Tables 1 and 2 leave no doubt about the fact that the higher the concentration of a sucrose solution, the more acceptable the fluid as revealed by a brief-exposure preference test. The brief-exposure method, of course, does not permit animals to approach satiation; consequently, it reveals a preference based mainly upon the immediate stimulation of head receptors, especially those of taste, touch, and smell.

Now in the 1-hr. preference test (Table 5) two factors, satiation of appetite and palatability, were operative and constantly interacting. The initial choice was determined by the head receptors. The rats persisted in accepting the 36-per cent solution, the preferred solution. When they became satiated or nearly satiated upon the 36-per cent solution, they were, we believe, cosatiated upon other sugar solutions, and, consequently, they took a minimum of the 9-per cent solution. This explanation implies that the level of acceptability depends upon two groups of factors—head receptor factors (palatability) and internal (including gastric) factors (satiation of a carbohydrate appetite).

SUMMARY AND CONCLUSIONS

1. The higher the concentration of sucrose solution, or the sweeter the solution, the higher is its level of acceptability as revealed by tests with the brief-exposure preference method. Scale values based upon results of preference tests show that the level of acceptability is directly proportional to the logarithm of the concentration.

2. In a 1-hr. drinking test with single sucrose solutions of 9-, 18-, or 36-per cent concentration, it was found that the quantity of fluid ingested varies inversely with the concentration. Analysis of the graphic records proves that the 9-per cent solution was accepted at a higher rate than the 36 at all times during the 1-hr. drinking test. Hence, if the quantity of fluid ingested or the rate of ingesting it is a criterion of acceptability, the 9-per cent solution is more acceptable than the 36.

3. Calculations indicate that the quantity of sucrose ingested and the quantity of water ingested during a 1-hr. test are functions of the concentration of solution. The intake of sucrose

is directly proportional to the concentration, and the intake of water is inversely proportional, i.e., the rats ingest more sucrose and less water at 36-per cent concentration than at 9. This result is contrary to a claim of Hausmann that the intake of sucrose is essentially independent of the concentration.

4. In a 1-hr. drinking test with two sucrose solutions presented simultaneously for choice, the rats took more of the 36-per cent solution than of the 9-per cent. The quantity of 36-per cent solution ingested when the two solutions were presented was only slightly less than the quantity ingested when the solution was presented alone; but the rats took from 2.3 to 20.6 times as much 9-per cent fluid when it was presented singly as when presented for choice with the 36-per cent solution.

5. In general, if the quantity of fluid ingested is employed as a criterion of the level of acceptability, a result may depend upon whether the fluid is presented alone or together with another fluid. Preference implies choice between two fluids; hence the single-stimulus method indicates relative acceptability but not true preference. Results obtained with the single-stimulus method cannot always be used for accurate predictions of preferences.

6. The discrepancies in results obtained with different tests of relative acceptability can be explained by making three assumptions. First, when a rat ingests a single food continuously, the food's level of acceptability falls from an initial level to zero with the approach to satiation of appetite; the quantity of food ingested is a measure of the quantity required to satiate *S* and to keep it satiated throughout the exposure period. Second, the relative acceptability of foodstuffs is at all times dependent upon their properties (such as concentration of solution, kind of food, texture, temperature, etc.), i.e., upon the stimulating pattern of the foodstuff. Third, if a rat is satiated on a high concentration of sugar solution, it is also at the same time satiated on lower concentrations.

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RELATIVE ACCEPTABILITY OF SACCHARINE SOLUTIONS AS REVEALED BY DIFFERENT METHODS

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The present paper is a report of tests upon the relative acceptability of saccharine solutions. The data and problems are related to another study upon the relative acceptability of sucrose solutions (3).

RELATIVE ACCEPTANCE OF SACCHARINE SOLUTIONS PRESENTED SIMULTANEOUSLY UNDER CONDITIONS OF SELF-SELECTION MAINTENANCE

In 1948–49, as part of an unpublished experiment, 19 albino rats were maintained upon a 17-component self-selection diet.[1] One cage housed 8 males and the other 11 females; all *S*s were about 6 mo. old at the time of the experiment.

After a period of habituation to the diet, six graduated bottles containing saccharine solutions were added at the end of each cage. The saccharine solutions were of the following percentage concentrations: 1.00, 0.50, 0.25, 0.13, 0.06, 0.03.[2] Daily intake of the six saccharine solutions and of the dietary components was recorded, and the average daily intake per rat was computed.

The experiment with the saccharine solutions continued for 27 days. During the first three days, however, several of the saccharine containers were drained dry, and larger bottles had to be substituted. For the following 24 days complete and accurate measures of daily intake were obtained with larger containers.

Figure 1 shows the average daily intake, in cubic centimeters, of the six saccharine solutions presented simultaneously to the 19 albino rats over a period of 24 successive days. Since differences between males and females were found to be extremely small and insignificant, the data for both sexes have been combined in a single graph.

Figure 1 shows a sharp peak of intake for the saccharine solution with a concentration of 0.25 per cent. Concentrations above and below this peak have markedly lower levels of intake. If the quantity of fluid accepted per day is taken as a criterion of acceptability, a concentration of 0.25 per cent is clearly the most acceptable saccharine solution under the dietary conditions described.

THE PREFERENCE OF THIRSTY RATS BETWEEN DISTILLED WATER AND A SERIES OF SACCHARINE SOLUTIONS

In another experiment six rats, three of each sex, were housed in group cages containing a very different diet. They were given unlimited access to tap water and Purina Rodent Chow. On alternate days, 24 hr. before a preference test, water bottles were removed from the cages. Immediately after each preference test the water bottles and *S*s were returned to the cages.

All preference tests were made by the brief-exposure preference method described elsewhere (1). Every trial offered *S* a choice between a sip of distilled water and a sip of saccharine solution. A test consisted of 50 successive choices (25 pairs) between water and a saccharine solution. Since six rats took the series of tests, there were 300 choices (150 pairs) for each concentration of saccharine.

Six concentrations of saccharine solution were tested, in descending order of percentage concentration, as follows: 2.4, 1.2, 0.6, 0.3, 0.15, 0.075. All percentages were prepared and specified by weight of solute and solvent.

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[1] The dietary components were: (1) casein; (2) corn oil; (3) sucrose solution of 38%; (4) distilled water; (5) di-potassium acid phosphate, 1%; (6) magnesium acetate, 0.5%; (7) calcium lactate, 2%; (8) sodium chloride, 3%; (9) a single mineral solution containing a trace of ferric chloride (.001%); manganese chloride (.001%); copper sulphate (.001%); zinc sulphate (.001%); potassium iodide (.00002%); cobalt sulphate (.00002%); (10) cod-liver oil; (11) thiamin hydrochloride, .004%; (12) riboflavin, .005%; (13) pyridoxine, .02%; (14) calcium pantothenate, .04%; (15) 1-inositol, .1%; (16) p-amino benzoic acid, .06%; (17) choline chloride, .1%.

[2] In this unpublished study a 1.00-per cent solution contained 1 gm. of saccharine in 100 cc. of solution. The saccharine solutions described elsewhere in this paper have been prepared and specified in terms of percentage concentration by weight, i.e., a 1.00-per cent solution contains 1 gm. of saccharine and 99 gm. of distilled water in 100 gm. of solution. This difference in method of preparation and specification of solutions makes no significant difference with concentrations as low as those here used.

In analyzing the data each *pair* of successive choices was rated as showing: (*a*) a preference for water, or (*b*) a preference for the saccharine solution, or (*c*) no preference.

The data are presented in Table 1. At the left the concentrations are arranged in descending order—the order in which they were presented to the rats. The last three columns show the number of pairs of choices indicating a preference for the saccharine solution, no preference, and a preference for water, respectively.

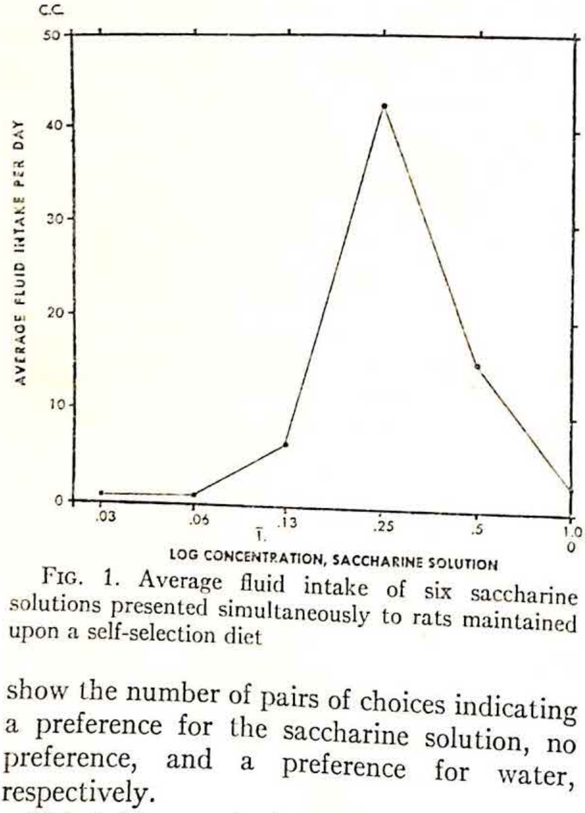

FIG. 1. Average fluid intake of six saccharine solutions presented simultaneously to rats maintained upon a self-selection diet

This table reveals that as the concentration of saccharine decreases, step by step: (*a*) the frequency of saccharine preference increases; (*b*) the frequency of water preference steadily decreases; and (*c*) the frequency of indiscriminate behavior increases.

The results give no indication of an optimum at 0.25 (between 0.3 and 0.15 per cent). On the contrary, within the range of concentrations tested, the lower the concentration of saccharine the higher the level of acceptability. If still lower concentrations had been used, an optimal concentration for the group would certainly have been found, since with subliminal concentrations no discrimination between the fluids is possible. This optimum, however, would be below 0.075 per cent and very much below 0.25 per cent, the optimal concentration found in the first experiment.

Further Tests with Saccharine Solutions

How can we explain the discrepancy in results? Why does one set of conditions yield an optimal concentration different from that obtained under other conditions?

In considering the problem we should recall that in experiments with solutions of sucrose, different methods of testing acceptability yielded different results (3). If the quantity of fluid accepted per day or per hour is taken as the criterion of acceptability, sucrose solutions show an optimum at about 9 per cent. If immediate choice is the criterion, there is no such optimum, but rats and men agree that the sweeter a solution is, i.e., the higher the concentration, the more acceptable it is. With sucrose solutions there is thus a discrepancy in results when concentrations are *above* the optimum. With saccharine solutions, in contrast, there is a discrepancy in results when concentrations are *below* the optimum.

TABLE 1

Preference between Distilled Water and Saccharine Solutions after 24 hr. of Water Deprivation

CONCENTRATION OF SACCHARINE (Per Cent)	PREFERENCE SCORE		
	Saccharine	No Preference	Water
2.4	1	51	98
1.2	9	48	93
0.6	24	64	62
0.3	30	87	33
0.15	21	115	14
0.075	35	112	3

In the hope of throwing light upon this discrepancy we made further tests with solutions of saccharine. The results will be briefly summarized:

First, to eliminate hunger and thirst, rats were maintained upon an unlimited supply of Purina Rodent Chow and tap water. They were given daily preference tests by the brief-exposure method. Three concentrations of saccharine solution were presented for choice in all possible pairs: 0.3-, 0.6-, 1.2-per cent concentration by weight of solute and solvent.

The total results for six rats, three of each sex, are summarized in Table 2. Each column shows the number of *pairs* of choices indicating a preference for the saccharine solution (0.3, 0.6, or 1.2 per cent) or no preference (=). It will be seen from the data that lower concentrations are markedly preferred to higher.

One might think that higher concentrations of saccharine would be sweeter than lower, but actually, to human taste, the higher concentrations are complicated by a quality (bitter?) that makes them less acceptable than the lower. The result of these tests, however, is in clear agreement with our expectation based upon the findings shown in Figure 1.

Second, ten, six-months-old rats, four males and six females, were given a series of 1-hr. drinking tests with saccharine solutions at the same three concentrations. Each test cage contained a standard cup with a single saccharine solution. Five rats took a series of tests in the ascending order of concentration: 0.3, 0.6, 1.2; the other five took the tests in the descending order: 1.2, 0.6, 0.3. Each concentration was tested for 12 days before a change was made. Rates of ingestion were recorded graphically throughout the 1-hr. test, but the graphic records are not utilized here. All animals were well fed and well watered at the time of the tests.

For the total group, the findings are summarized in Table 3.[3] It is clear from these results that the 1.2-per cent solution was ingested in smaller quantity than the other two. With this method, however, there was a tie between the 0.3- and 0.6-per cent solutions. Some animals took more of 0.3 and others more of 0.6. Differences were small and often not significant.

TABLE 2

Results of Preference Tests with Three Saccharine Solutions

TEST NUMBER	SACCHARINE CONCENTRATION								
	0.3	=	0.6	0.3	=	1.2	0.6	=	1.2
1	21	25	4	25	18	7	13	28	9
2	27	17	6	33	13	4	23	22	5
3	27	22	1	31	14	5	24	21	5
4	27	19	4	36	12	2	33	14	3
5	21	27	2	39	10	1	36	12	2
Total.........	123	110	17	164	67	19	129	97	24

TABLE 3

Intake of Single Saccharine Solutions during 1-hr. Drinking Test

CONCENTRATION (Per Cent)	AV. GRAMS OF SOLUTION INGESTED	STANDARD DEVIATION (Grams of Solution)
0.3	12.2	4.2
0.6	12.6	4.8
1.2	7.5	4.4

TABLE 4

Intake of Two Saccharine Solutions during 1-hr. Preference Test (two-day total)

CONCENTRATION (Per Cent)	AV. GRAMS OF SOLUTION INGESTED	STANDARD DEVIATION (Grams of Solution)
0.3	7.4	3.3
1.2	3.6	2.7

One possible explanation of this tie, in line with other findings, is that the location of the optimum varies with dietary conditions. With a Purina–tap-water diet the optimum may be within or below the range of 0.3- to 0.6-per cent concentration. This suggestion that the optimum depends upon the diet is in line with some unpublished work with salt solutions at the University of Illinois by Mr. Harold W. Richey.

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[3] To conserve space, individual data on range of intake and average intake of each animal for each solution are contained in a table filed with ADI Auxiliary Publications Project, Photoduplication Service, c/o Library of Congress, Washington 25, D. C., and may be obtained from them by ordering Document 4018, remitting $1.25 for microfilm or $1.25 for 6 x 8-in. photocopies.

Richey offered rats a continuous choice among several solutions of sodium chloride. The rats were housed in individual cages and maintained upon a Purina diet and tap water. Under these conditions the individual optima changed unpredictably within the range of 0.7 per cent to 0.0 (distilled water); the optima were at times stable and at times changeable, but there seemed to be little law and order to the phenomena. When, however, the same animals were placed upon a self-selection diet identical with that used by Young and Chaplin (2), the rats at once revealed a sharp and consistent optimum at 0.7-per cent NaCl. The work demonstrated clearly that a fixed optimum is dependent upon the diet.

In the initial experiment (above), with saccharine solutions, the self-selection diet was almost identical with that employed by Young and Chaplin. The sharp saccharine intake curve shown in Figure 1 is very similar to the intake curves for salt solutions described by Young and Chaplin. It is likely, therefore, that an optimum varies with dietary conditions and that results represented in Figure 1 depend upon a particular diet.

Third, a 1-hr. drinking test of preference was run with two saccharine solutions, 0.3 and 1.2 per cent, presented simultaneously for choice. The test was run for two days with both spatial arrangements of the cups.

For the group of 10 rats the data have been pooled and are presented in Table 4.[4] The rats individually all ingested more of the saccharine solution with the *lower* concentration.

This result agrees with predictions based upon the data of Figure 1 and also upon the preference data in Table 1. In this connection it should be recalled that in a similar preference test with sucrose solutions rats selected the *higher* concentration (3). In that test, however, the two criteria of preference (quantity of fluid ingested and immediate choice) would lead to opposed predictions, whereas here the two criteria are in agreement and lead to the same prediction.

CONCLUSION

The location of an optimal concentration for saccharine solutions is dependent upon the method employed in determining the optimum and probably also upon the dietary conditions under which it is located. If rats are maintained upon a self-selection diet and given a continuous choice among six saccharine solutions presented simultaneously, a sharp optimum at 0.25-per cent concentration is found. If thirsty rats, maintained upon a Purina diet, are tested with the brief-exposure preference method, in a series of choices between distilled water and saccharine solutions of different concentrations, the optimal concentration is less than 0.075-per cent concentration.

It is here proposed that the term *acceptability* be employed in an objective sense without bias as to determining conditions. Previous experiments have demonstrated that relative acceptability of test foods depends upon intraorganic conditions (appetitive factors), upon stimulus-receptor conditions (palatability factors), and upon dietary history (food habits and addictions).

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[4] Individual data are contained in Document 4018 filed with ADI. See footnote 3.

EFFECTS OF CORTICAL LESIONS ON ESTABLISHED HOARDING ACTIVITY IN RATS[1]

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Experiments during recent years (5, 7, 8, 9) have demonstrated that the hoarding activity in rats can be systematically investigated in the laboratory. A good deal of information has been assembled about the experimental conditions under which this activity takes place. At the present time little is known, however, about the underlying motivational and physiological factors which determine this behavior. There is sufficient evidence to suggest that hoarding is at least partly motivated by inborn patterns of behavior, and it might be assumed that these are controlled by physiological mechanisms.

Somatic influences on behavior patterns may be investigated by determining the effects of cortical lesions on the behavior. Lashley (2), for example, has demonstrated the relationship between the extent of lesions and the animal's loss of learning ability, and Beach (1) has investigated lesion effects on maternal behavior. It was found in both these investigations that larger cortical lesions resulted in increased loss of the investigated behavior pattern. Zubek (10), on the other hand, found that cortical lesions may increase hoarding activity. He applied, however, fairly small lesions, 6 per cent to 27 per cent of the neocortex, and the resulting increases in hoarding were relatively small. It seems desirable, therefore, to investigate the effects of larger cortical lesions (25 per cent to 40 per cent of the neocortex) on hoarding behavior.

METHOD

Apparatus and Animals

A modification of the "closed alley" hoarding apparatus (9) was used. The home cage of each rat had a sliding door which, when opened, gave the animal access to a 40-in. long alley at the end of which was a food bin which contained a number of Purina Lab Chow pellets of approximately uniform size. The experimental room was uniformly lighted and had a daily temperature recording ranging between 74° F. and 82° F. The alleys were painted with aluminum paint in order to give approximately uniform illumination.

Thirty-one adult rats were used for the experiment, 25 of them laboratory-bred Sprague-Dawley females, and 6 males of an inbred local (white Norway rat) laboratory strain. These animals had been given preliminary hoarding trials of 7 to 21 days in order to determine their hoarding activity. The weight of each rat was recorded once a week.

Procedure

Hoarding trials. The preoperative experiments consisted of 11 daily hoarding trials which followed the preliminary ones. Forty minutes before each trial *S* was given two pellets to eat in its cage. The sliding door was then opened for a 25-min. period during which *S* had access to its alley. All pellets were taken from the cage at the time of opening of the doors and again at the end of the hoarding trial, when they were counted. The lights in the room were turned on automatically 1 hr. before the feeding period and were turned off after 12 hr. It was possible to vary the time of hoarding whenever necessary because there was no other illumination in the room. The number of pellets hoarded during each of the last 10 days of this period was the basis for the preoperative hoarding scores.

The *Ss* were divided into an experimental group (21 rats) and a control group (10 rats), which had approximately the same means and standard deviations of hoarding scores. As a consequence of the operative procedures 2 *Ss* were lost, so that the postoperative trials were conducted with 20 experimental and 9 control *Ss*.

After the operation, *Ss* were returned to their home cages, where they received unlimited feeding. Postoperative hoarding trials started 51 days after the last preoperative trial. They consisted of 22 daily trials conducted according to the same schedule as the preoperative ones. Hoarding scores for a 10-day period served as the basis for subsequent computations. This period began for each *S* after it had hoarded for 4 or 5 days, because not all *Ss* started to hoard on the same day and each *S*'s scores during the first days of hoarding showed usually a great deal of variability (8). The mean daily hoarding scores for each of the two groups of rats remained fairly constant during this 10-day period.

Operative procedures. The experimental *Ss* were operated under pentobarbital (30 mg/kg body weight) and ether narcosis. After the skull had been widely exposed, it was opened bilaterally with a trephine, and the opening was enlarged with small bone cutters. The dura was then cut, and the desired amount of cortex was removed with a curette. The skin was subsequently sutured and covered with collodion. Three of the control animals (No. 17, 20, and 21) underwent sham operations in which one trephine hole was placed in the skull, but no cortex was removed.

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[1] This investigation was supported in part by a research grant from the Hixon Fund.

Determination of lesions. After the hoarding experiment was terminated, the brains of the operated rats were fixed by perfusion. The abdominal aorta was cannulated and tied off caudally. After the right ventricle of the heart had been cut, Ringer's solution and then 70 per cent alcohol solution were injected into the cannula until the upper part of the rat's body became stiff. The brain was then removed, placed in 100 per cent alcohol for 48 hr., in Xylol for 24 hr., and imbedded in paraffin. Sections of 25μ were cut, and every twentieth section was mounted and stained with toluidine blue. Alternate sections were then sketched under a projector, where structures defining brain levels were identified and the extent of cortical lesions was marked. The dimensions of the lesions in each section were then transferred by proportional measurements to the appropriate level of the section on the dorsal and lateral brain diagrams. The areas of the cortical lesion were marked, measured by a planimeter, and expressed as the percentage of the total area of the neocortex. The brains were finally examined for subcortical damage, the extent of which was recorded.

Treatment of hoarding data. Since the measure, "number of pellets collected," did not lend itself well to statistical analyses, these scores were converted to deci-log units (DLU), following the suggestion of Morgan (6). The DLU score was obtained by adding one unit to the number of pellets hoarded in each trial, finding the logarithm, and multiplying by ten. These scores were then used as the basis for statistical analysis.

RESULTS

Effects of Brain Lesions on Hoarding

The hoarding scores for each *S* of the control group are shown in Table 1. These are the mean scores (DLU) of the 10 trials before the operation and of the 10 trials during the postoperative period. This table indicates a general decline in hoarding scores during the interval between the two experimental periods. The significance of the decline of the mean for the total group (1.09 DLU) was determined by computing the *t* ratio for the mean of the difference between hoarding scores ($t = 2.44$), which is significant at the .05 level of confidence. Two *S*s (No. 40 and 30) showed significant reductions (at the .05 level) of their hoarding scores during this period. The decline in hoarding scores of the control group might be explained by the unavoidable increase in mean room temperature, from 76° F. to 80° F., between the two experimental periods, for it has been observed that higher environmental temperatures tend to reduce hoarding activity (4).

Table 2 shows the mean hoarding scores and their standard deviations (for 10 trials) for each of the experimental *S*s. None of these *S*s increased its hoarding activity as the result of brain damage, and most exhibited considerable hoarding loss. In order to determine the hoarding loss for each *S*, a "deficit index" was computed which is the ratio of the amount of loss to the preoperative hoarding score. Table 2 is arranged in the order of increasing deficit index, which is shown to range from 0.01 to 1.00. The significance of the hoarding loss for each *S* was found by computing the *t* ratio for the difference between mean preoperative and mean postoperative hoarding. Table 2 shows that for 15 of the 20 *S*s the decrease of mean hoarding scores was significant beyond the .01 level of confidence, and for 2 additional *S*s it was significant beyond the .05 level.

TABLE 1

Hoarding Data for Control Group

RAT NO.	MEAN HOARDING SCORE (DLU)	
	Preoper.	Postoper.
40	11.17	8.12
20	14.69	14.27
30	15.70	13.05
17	16.26	16.66
31	16.33	17.17
22	16.98	16.80
39	17.61	16.23
42	18.63	17.07
21	18.81	16.94
Mean.	16.24	15.15

The mean preoperative hoarding scores for the control and experimental groups were 16.24 and 16.12, respectively, and the difference between these is not significant ($t = 0.123$). The corresponding postoperative scores were 15.15 and 10.95, respectively, and the difference between these is significant beyond the .05 level ($t = 2.96$). The median hoarding score for all *S*s prior to the operation was approximately 16.5. Computations of a contingency table for the experimental *S*s which hoarded more than 16.5 and less than 16.5, before and after the operation, respectively, gave a chi-square coefficient of 5.40, which was significant at the .02 level. A similar computation for the control group showed no significant differences. In these computations Yates's corrections for continuity were applied. It may therefore be concluded that the experimental *S*s hoarded significantly less postoperatively than did the controls. The evidence indicates that cortical damage causes a significant decline in hoarding activity, which is, however, not altogether eliminated, but continues regularly at a reduced level.

TABLE 2

Hoarding Data for Experimental Group

RAT NO.	HOARDING SCORE (DLU) FOR 10 TRIALS				DEFICIT INDEX	p	CHARACTERISTICS OF CORTICAL LESIONS		
	Preoperative		Postoperative						
	M	σ	M	σ			% Removed	Mid-line*	Total at Mid-line*
33	16.83	0.87	16.73	1.25	0.01	>.05	35	10	6
43	14.55	2.98	13.96	1.00	0.04	>.05	37	7	9
16	15.37	1.30	14.45	0.78	0.06	>.05	29	12.5	6
41	19.96	0.21	18.06	1.11	0.09	.01	38	9	5
38	18.97	0.64	17.08	2.09	0.10	.05	36	11	14
24	16.11	1.58	12.60	1.30	0.22	.01	28	10	9
15	16.68	1.00	12.87	1.25	0.23	.01	26	11	6
23	18.14	1.10	13.91	1.70	0.23	.01	32	11	7
29	18.14	0.31	13.08	1.38	0.28	.01	33	10.5	13
18	8.55	1.60	6.02	2.69	0.29	.05	23	9.5	3
14	16.31	1.26	11.42	0.94	0.30	.01	31	8.5	14
36	18.18	0.75	11.77	2.25	0.35	.01	37	8	11
19	17.08	0.97	10.92	2.14	0.36	.01	40	12	11
44	15.99	0.58	9.67	0.97	0.40	.01	33	12	13
34	17.60	0.37	10.37	1.95	0.41	.01	50	9	16
37	13.06	4.97	6.85	1.99	0.48	.01	38	7	13
46	14.82	1.34	7.20	1.38	0.51	.01	30	13	5
32	16.85	0.63	6.51	1.88	0.61	.01	32	7.5	13
27	17.52	1.47	5.46	1.34	0.69	.01	35	9	12
35	11.72	0.82	0.00	0.00	1.00		25	12	11
Mean........	16.12		10.95						
σ	2.57		4.42						

* According to levels of diagrams, Figure 1.

Effects of Specific Brain Lesions

The location and extent of each cortical lesion are shown in Figure 1 and Table 2. Since the deficit indices varied considerably for the group of experimental *S*s, an attempt was made to relate it to a number of variables of the cortical lesions. The size of the lesions ranged from 23 to 50 per cent of the neocortex, although only one *S* had a lesion larger than 40 per cent. Within this relatively narrow range of lesions it was not possible to discern any relationship between the size of lesion and the amount of hoarding deficit; the rank-order correlation between these two variables is .10, which is not significant.

It was not attempted to obtain accurate localization of the lesions on the cortical surface. As can be seen from Figure 1, lesions were placed on different areas along the frontal-caudal direction of the cortex, and the composite diagram indicates that most areas of the cortex were subjected to cortical damage. The approximate location of each lesion on the cortical surface is indicated by the mid-line of the lesion (according to the levels of the diagrams), which is shown in Table 2. This localization does not appear to be related to the hoarding deficit; placement of cortical

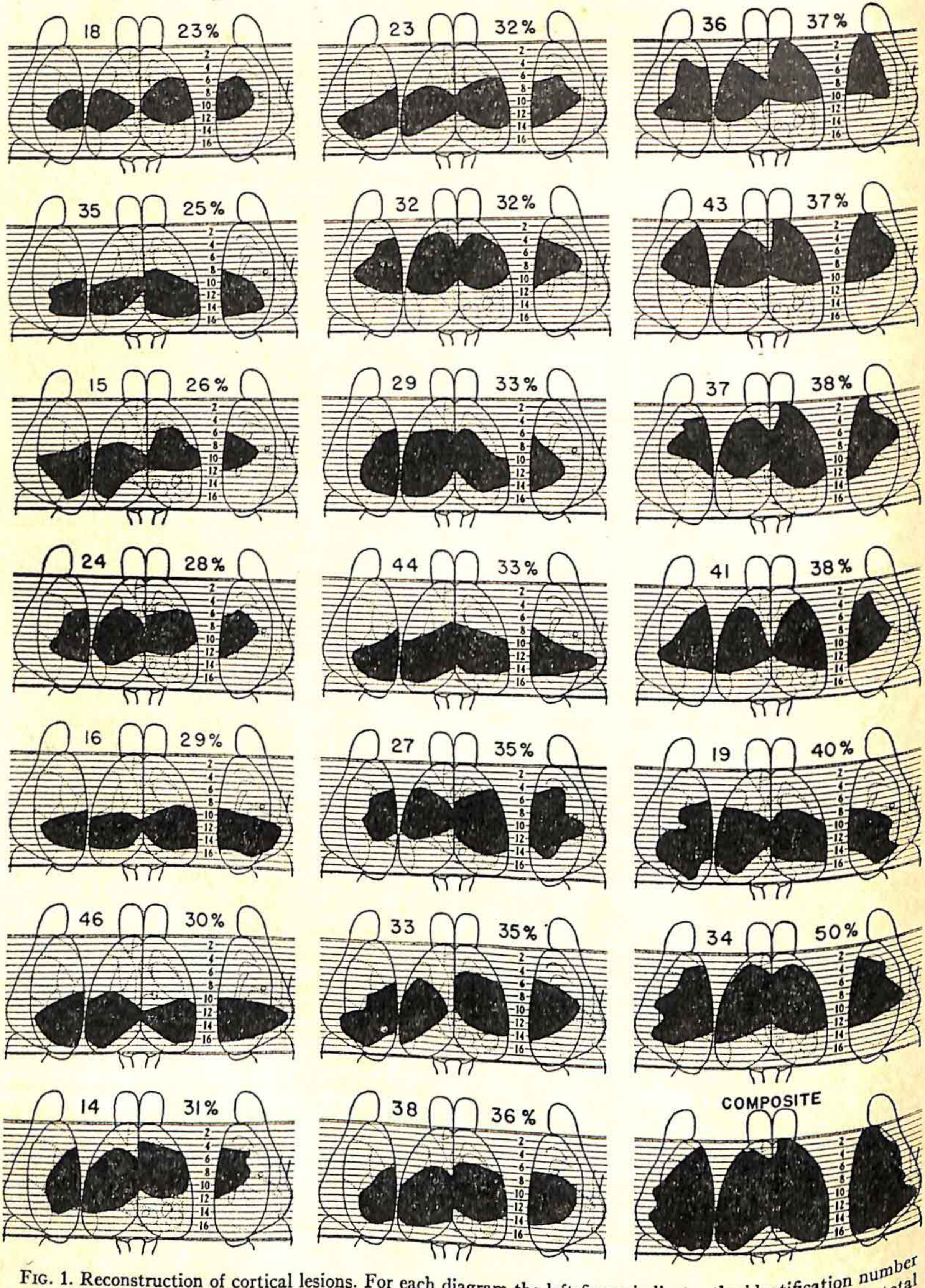

FIG. 1. Reconstruction of cortical lesions. For each diagram the left figure indicates the identification number of the animal, the right figure the percentage of neocortex removed. The composite diagram shows the total cortical area explored in this study.

lesions at any level of the cortex seems to be equally effective.

When the histological sections were examined for subcortical lesions, it was found that in some *S*s areas in the striatum or the anterior thalamic nucleus were damaged. During the postoperative hoarding trials two *S*s (No. 34 and 27) exhibited difficulties in locomotor coordination, although only No. 27 could not readily pick up the pellets. Both these *S*s showed damage in the posterior striatum. There were also indications of subcortical damage in other *S*s. Computations of a chi-square coefficient between degree of subcortical damage (none, slight, or clear-cut damage) and hoarding deficit did not indicate any significant relationship between these two variables ($\chi^2 = 1.9$).

The possibility was investigated that cortical lesions along the median line of the brain (Lashley's areas *c*, *f′*, *aa*, and *m′*) bore a relationship to the hoarding deficit. The lengths of these lesions according to the levels of the cortical diagrams were determined, and the sums of these for the right and left hemispheres of each *S* are shown in Table 2. A product-moment correlation coefficient between these and the deficit indices was found to be 0.445. Rat No. 35 was omitted from these calculations since it did not hoard at all postoperatively, and its score was therefore discontinuous with the distribution of scores for the other *S*s. The significance of this correlation coefficient was determined by computing its *t* ratio ($t = 2.35$) which is significant at the .02 level of confidence. Computations of a contingency table[2] between the lengths of these lesions and the deficit indices yielded a chi-square coefficient of 8.95, which is significant well beyond the .01 level.

The possibility was examined that cortical lesions were less effective in rats in which hoarding is well established than in those which hoard little. Since there was a substantial range in the original hoarding scores for the *S*s, these were correlated with the deficit indices. The product-moment correlation coefficient between these variables is −.10, which is not significant.

DISCUSSION

The results of this investigation show clearly that cortical lesions tend to reduce the hoarding activity in rats without eliminating it altogether. Hoarding activity, as Marx (5) has pointed out, is by no means a simple phenomenon, and the amount of pellets collected is only one measure of this behavior. Observations were made on some of the other aspects of this activity, such as speed of hoarding, latency of onset of hoarding, and maintenance of stereotyped behavior. With the exception of two *S*s which had damage in the striatum, the hoarding process proceeded without difficulty. The speed of hoarding, i.e., the time required for one round trip, was measured frequently and found to be about 5 sec. during both the preoperative and the postoperative trials. The decrease of hoarding was therefore not caused by slower activity or by sensory or motor deficit resulting from the lesions. It has also been observed (3, 5) that each rat follows a characteristic pattern of hoarding behavior which differs from that of other rats. Although no detailed protocols were recorded, it was observed, for example, that rats which preoperatively went on many "dry runs" continued this pattern postoperatively. One notable exception to this persistence of stereotyped behavior was observed, namely, six experimental *S*s exhibited "alley hoarding" during the first two or three days of their postoperative hoarding activity. They deposited the initial four to six pellets during each trial in front of the cage and then left the additional pellets inside the cage. After about three days they resumed their regular hoarding procedure. This activity was not observed in these *S*s during the preoperative trials, nor did any of the control animals behave in this manner.

The decline of hoarding as a consequence of cortical lesions seems to be in general agreement with the results of similar investigations of other types of behavior, such as maze learning (2) and maternal behavior (1). Since the former represents learned behavior and the latter is instinctive, one would expect that hoarding activity, which probably consists of both inborn and learned components, would also be reduced by brain lesions.

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[2] The cutting-off points were the median values for both variables.

The results of this investigation do not support the principles of "mass action" (2) of the cerebral cortex. The range of the size of the lesions was quite small, whereas the original hoarding scores varied considerably. In order to determine the effect of the size of brain lesions on hoarding activity, it would be necessary to select *S*s which had little variability in their preoperative hoarding and then to apply lesions of a wide range of size.

The correlation coefficient of .445 between deficit index and length of cortical lesion along the median line of the brain suggests that a relationship exists between these variables. A correlation coefficient of this magnitude is, of course, not impressive, and subcortical lesions of some *S*s may have increased it spuriously, although subcortical lesions themselves did not significantly influence the deficit index. On the other hand, since the amount of median cortex removed was only between 9 per cent and 50 per cent of the total length of this area (assuming the length of each median strip to be 16 levels of the diagram), larger lesions along this strip might have increased the magnitude of the correlation coefficient.

There has been no systematic investigation of the functional significance of the median cortex in the rat. In Lashley's investigations (2), for example, this region constituted only a small portion of the lesions, so that its function was not readily discernible. Almost none of the cortical lesions in Zubek's investigation (10) included this area, and the size of these lesions was, moreover, considerably smaller than the ones in the present investigation. The increase in hoarding which Zubek found was smaller than the decrease obtained in this investigation. Computations of an "increase index" for the former investigation gave an average of about 0.1, whereas the average deficit index in the present investigation is approximately 0.3. The difference between these figures is considerable, particularly since they are based on logarithmic data. It is therefore not inconceivable that small cortical lesions excluding the median cortical strip increase hoarding activity, whereas larger lesions including this cortical area result in hoarding deficit.

The results of this investigation suggest further research into the functions of the median cortical area. One should apply relatively small lesions, localized in this portion of the cortex, and determine their influence on hoarding activity.

SUMMARY

Bilateral cortical lesions (23 per cent to 50 per cent of the neocortex) were applied to a group of 20 rats. Their hoarding activity was determined before and after the operation. Nine rats served as a control group which did not undergo brain operations.

1. There was a decrease in hoarding by the experimental rats as a result of the operation; their postoperative hoarding was significantly less than both their preoperative hoarding and the hoarding of the control rats.

2. The hoarding loss was not related significantly to the size of the lesions, their general location on the cortical surface, subcortical damage, or the amount of preoperative hoarding.

3. A correlation coefficient of 0.445 was obtained between the magnitude of hoarding deficit and the extent of the lesions along the median line of the brain. This coefficient was statistically significant. It is suggested that the cortical strip along the median line of the brain may be of special significance to behavior such as hoarding.

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EFFECTS OF INTENSE LIGHT STIMULATION ON SOUND-INDUCED SEIZURES IN RATS

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This experiment is concerned with the effects of an intense light stimulus upon the incidence, latency, and severity of seizures induced in rats by a simultaneous sound. It also tests the hypothesis that seizures may be precipitated by light alone. Although it has been established that the potency of a tonal stimulus is a function of its effective intensity (4, 5), there has been little systematic interest in the results of intense excitation of other modalities.

METHOD

Subjects. The *S*s for this investigation were 200 albino and hooded rats from 50 to 150 days of age. The animals were maintained on a diet of Purina Laboratory Chow supplemented at times by cod-liver oil.

Apparatus. A 14-in. cuboidal box, painted white inside, was constructed of plywood and Acousticelotex. Inside the box was placed a floored glass cylinder 12 in. high fashioned from a 5-gal. carboy. At each of four corners between the box and the glass test compartment a photoflood bulb, General Electric No. 1, was mounted in an upright position. A battery compartment for a 3-in. doorbell formed the lid of the box. The doorbell was mounted on the underside of the lid and covered with stiff hardware cloth. When the box was closed, the hardware cloth formed a tight cover for the test compartment. At times when the photofloods were not in operation, the inside of the box was dimly illuminated by a flashlight bulb. During light-exposure periods *E* watched the animals through an additional dense filter.

Procedure. With negligible exceptions the rats were run in groups of 20. At least two days elapsed between successive tests. Every animal was exposed to each of four conditions of stimulation. In one of these the test compartment was strongly illuminated for 30 sec. by the battery of photoflood lights. In another, the bell was sounded alone for 1 min. The third and fourth conditions combined light and sound stimulation, with photofloods in operation during the first or second half of the sound-exposure period.

The lights could not be turned on for the full minute because of the heat produced. To control the effects of build-up of temperature within the box, each group of 20 animals was divided into four subgroups. These subgroups were tested in different orders, and were tested once in each position within the order. The balancing technique can be visualized as a 4 by 4 latin square with conditions of stimulation assigned to columns, order of testing assigned to rows, and subgroups assigned to letters. Between tests given to each subgroup the box was aired for 5 min.

Observations showed that the animals kept their eyes open during exposure to light. To check the possibility that they were rapidly blinded, five rats which had been trained in a Grice (2) black-white discrimination apparatus were stimulated for 35 sec. Subsequent tests of retention indicated that discriminative capacity was unimpaired.

A seizure was defined as a running fit followed by suppression of tactile placing responses (1). Latency was measured from the onset of the auditory stimulus to the beginning of the running fit. A severe seizure was defined as one which included tonic or clonic components.

RESULTS

Of the 200 animals tested 37 per cent responded one or more times. A total of 163 seizures, 79 of them severe, was observed in 800 exposures. No seizures were elicited by the photofloods alone. Stimulation by the bell alone yielded 52 attacks, and bell plus light in the first and second halves 60 and 51, respectively. Chi square for the latter three values is .89, which corresponds to a p value between .50 and .70. Among subgroups tested first, second, third, and fourth there were 38, 38, 36, and 51 seizures. Chi square for these values is 3.5, for a p value between .30 and .50.

The median latency for seizures in the bell-alone condition was 47 sec., and comparable scores for combined conditions with light at the beginning and light at the end were 48 and 44 sec., respectively. Latency scores were similarly stable from one part of a test session to another, for the median values were 47, 46, 49, and 43 sec. in the first to last periods, respectively.

There were 22 tonic-clonic seizures to the bell alone, 30 under conditions in which light and bell began simultaneously, and 27 where the light came on during the second half of the bell-exposure period. Chi square is 1.24 and not significant. The trend for scores in successive test periods is somewhat more impressive, with frequencies of 13, 18, 19, and 29 for the first to last, respectively. Chi square for these values is 6.82, and the corresponding p value is between .05 and .10.

DISCUSSION

An intense visual stimulus does not readily precipitate convulsive seizures in rats. It is true that the duration of the exposure was short. Yet comparable exposure periods with the bell, as judged from latency data, produced 30 attacks. The results thus support the specificity implied by the terms "audio-epileptic" (7) and "audiogenic" (6).

However, incidental observations suggest that the precipitating excitation is not carried by the auditory pathway. The most notable of these is the trend of increasing severity of seizures as a function of test-compartment temperature. If this facilitation is real, it is probably a result of pinna irritation. Although the central portions of the test compartment were never uncomfortable to the human hand, the ears of the rats were so sensitive that they usually became extremely red and often were edged by blistering burns. It is interesting to note that during exposure to light the rats typically licked their paws and then rubbed saliva on their ears. This response was similarly elicited by an electric radiant heater placed on top of the test compartment.

These facts seem significant because the anterior pinna is supplied by a branch of the mandibular division of the trigeminal nerve. The same branch is also distributed to the drum membrane, a structure which figures prominently in the "nocigenic" theory of seizure initiation that has been proposed by Marx and Jurko (3). They suggest that the relevant excitation is carried not by the auditory pathway, but by extra-auditory pain pathways which begin at the drum membrane.

The Marx and Jurko hypothesis was advanced to account for sensitization to seizures which accompanies secretory inflammation of the middle ear. Under these circumstances they suppose that increased tension on the drum membrane lowers the thresholds of pain receptors. It is possible, of course, that middle-ear disease sensitizes auditory receptors. However, it is quite unlikely that irritation of the pinna could have such effect, and the latter kind of facilitation would be reasonable in terms of summation of excitation carried by adjacent pain pathways.

It should be emphasized that this support for the nocigenic theory is largely speculative. None of the observations is statistically demonstrable at an acceptable level of confidence. Nevertheless, each of the changes noted is in an appropriate direction. For example, the largest fluctuations in frequency and severity scores are obtained when the light is present during the first half of the bell-exposure period. In any event, the data suggest that the hypothesis is a fruitful one and readily testable with further straightforward operations.

SUMMARY

This experiment examined the effects of an intense light stimulus upon the incidence, latency, and severity of seizures induced in rats by a simultaneous auditory stimulus. Further, it provided a test of the hypothesis that convulsive attacks could be precipitated by a light alone. Each of 200 animals was tested under conditions of light stimulation alone, bell stimulation alone, and combined light and bell stimulation. The visual stimulus was provided by a battery of photoflood lights which surrounded a glass test compartment.

No seizures were produced by light alone, nor did the light have statistically demonstrable effects upon sound-induced seizures. There was a tendency of borderline statistical significance for seizures to be more severe with increases in test-compartment temperature. It was suggested that such facilitation could be attributed to irritation of the ears of the animal. This effect, if a real one, is most readily interpretable in terms of a nocigenic theory of precipitation.

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DOES TETRAETHYLAMMONIUM REDUCE FEAR?

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In a recent paper, Auld (1) reports the depressing effects of tetraethylammonium chloride (abbreviated hereafter as TEA) upon the running speed of rats in a Miller-type escape-avoidance situation. The author argues that this decrement is to be explained by a reduction in the "drive of fear" motivating the escape habit as a result of partial blocking of the autonomic ganglia by TEA. The behavioral tests employed in these experiments place considerable emphasis on locomotion or motor performance, however, and the need for a more direct experimental control for the possible effects of TEA upon the motor capacities of rats is apparent.

The present report describes two experiments designed to investigate further the alleged fear-reducing properties of TEA. The first experiment tests the effect of TEA on a fear-motivated response defined by its depressing effect upon a previously established lever-pressing habit. In this situation, fear reduction by TEA could be expected to lessen the depressing effect of the fear response upon the lever-pressing habit, thus providing an inherent control for the effects of the drug upon the motor capacities of the organism. The second experiment tests the effect of TEA upon locomotor activity and upon the speed of a running response motivated by drives other than fear (hunger, thirst) in order to provide some information on the more general effects of the drug upon behavior.

EXPERIMENT 1

Method

Subjects. Twelve male albino rats, approximately 100 days old at the start of the experiment, were *Ss*.

Apparatus and procedure. A conditioned emotional response of the "fear" or "anxiety" type was superimposed upon a previously learned lever-pressing habit in all animals according to a procedure previously described by Hunt and Brady (3). First, thirsty animals were trained to press a lever for an aperiodic water reward. Then, when their lever-pressing curves became stable, the "fear" response was conditioned in six daily trials. Each trial consisted of a 3-min. presentation of a clicking noise, as the conditioned stimulus, terminated contiguously by two momentary, painful, electric shocks to the feet. All conditioning trials were conducted during the animal's normal daily lever-pressing runs and were spaced several days apart, with normal adaptation lever-pressing trials intervening in order to reduce the frequency with which the rats developed generalized fear reactions to the apparatus. After six such emotional conditioning trials, the response developed as a complete cessation in lever pressing during presentation of the conditioned clicker stimulus accompanied by immobility and defecation in all animals.

Twenty-four hours after the last conditioning trial, when all animals had acquired the emotional response, a test was conducted in order to determine the effects of TEA upon this fear-motivated habit. In accordance with Auld's procedure, the animals were divided into two equal groups matched for both speed of acquisition of the emotional response and strength of the lever-pressing habit. All animals of the experimental group received intraperitoneal injections of tetraethylammonium chloride in aqueous solution (12.5 mg/cc). The dosage was 31 mg/kg of body weight. All animals of the control group received volumetrically equivalent injections of normal saline solution. Twenty minutes were allowed after injection for the drug to reach maximal concentration in the rats' blood stream before the animals were placed in the lever-pressing apparatus and tested for their reaction to the conditioned clicker stimulus. Following this test, all animals were returned to their home cages where they were permitted free access to food and water without trials of any kind for one week, at which time a second test was conducted. During this second test, the six animals which had previously served as controls were now injected with TEA, while the former TEA animals of the first test now served as controls.

Results

The results of these critical tests revealed quite marked differences between the TEA-injected animals and the controls. First, as would be expected, the normal saline had little effect upon either the lever-pressing habit or the conditioned emotional response. The control animals produced typical lever-pressing curves, and presentation of the conditioned clicker stimulus resulted in crouching, defecation, and complete cessation of lever pressing in all animals of the control group. In marked contrast, however, none of the TEA-injected animals made a single lever-pressing response at any time during either of the two critical test trials. On both occasions, the six animals in this experimental group remained almost completely immobile throughout the entire 15-min. run in the lever-pressing apparatus, and on both tests presentation of the conditioned clicker stimulus produced defecation in five of the six TEA-injected rats.

These results suggested that the more generalized effects of TEA upon locomotion or motor performance in rats might well be critical in accounting for both the results obtained in the present experiment as well as those reported by Auld. Indeed, an interpretation of the depressing effects of TEA upon a fear-motivated running response in terms of inferred "fear reduction" would appear to be considerably less parsimonious than a more operational "activity reduction" hypothesis if it could be demonstrated that (*a*) locomotor activity is significantly reduced in rats following TEA injection, and (*b*) running responses motivated by drives other than fear (hunger, thirst) are also depressed following injection of TEA. In order to test these two possibilities, a second experiment was performed.

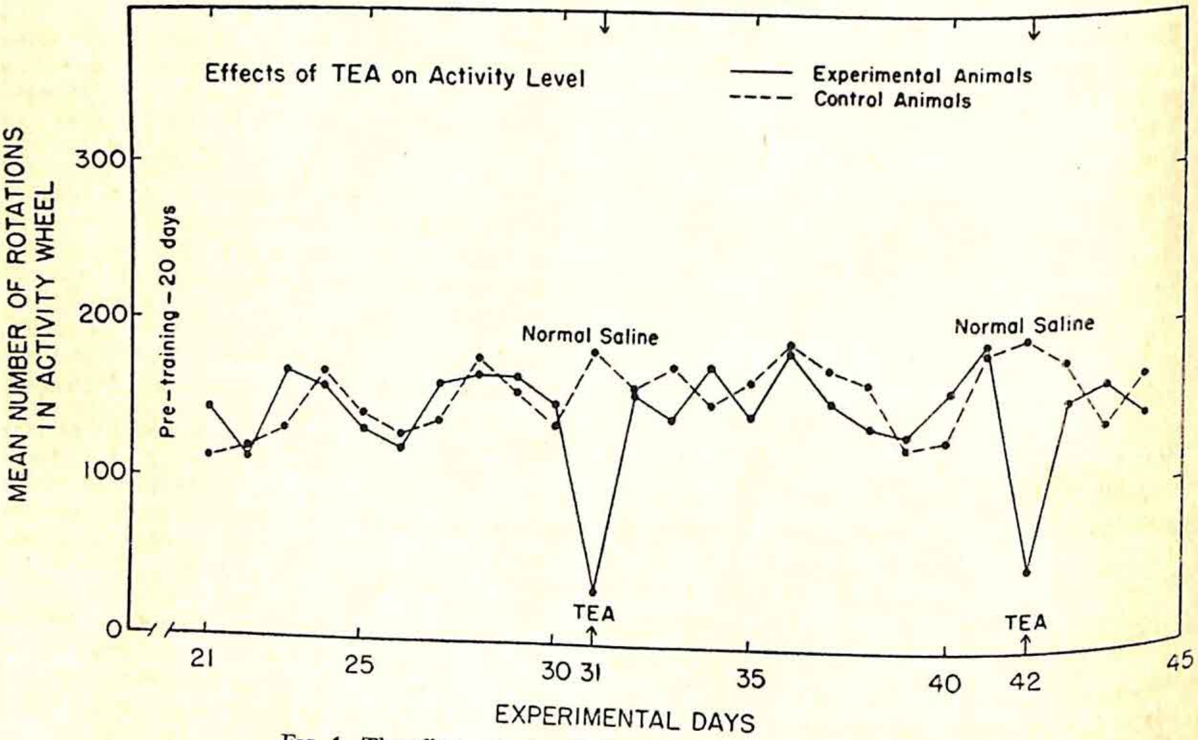

FIG. 1. The effects of tetraethylammonium on activity level

EXPERIMENT 2

Method

Subjects. Twelve male albino rats, approximately 100 days old at the start of the experiment, served as *Ss*.

Apparatus and procedure. During an initial 20-day pretraining period, the animals were placed on a 22-hr. food- and water-deprivation schedule and received daily trials in a Wahmann-type activity wheel, and in an 8-ft. straight runway situation according to the following general procedure. First, each animal was removed from its home cage and placed in the activity wheel for 20 min. Then the animal was removed from the activity wheel and placed in the starting box of the straight runway. During this initial training period, the sliding doors of both the starting box and the goal box of the runway were removed, *S* was permitted to explore freely for a 20-min. period during which time both food and water were accessible in the goal box. Upon removal from the runway, *S* was permitted free access to food and water for 2 hr. in a feeding cage, after which it was removed to its home cage to await, without food or water, the following day's trials.

From experimental day 21 through day 30, daily recordings were made of each *S*'s activity in the rotating drum during the 20-min. trial and of each *S*'s initial running time from starting box to goal box in the runway. The general procedure followed for the runway trials during this 10-day recording period was to place the animal in the starting box with the door opening into the runway closed. After a 10-sec. delay, the door was raised simultaneously with the starting of a stop watch. When the animal entered the open door of the goal box, the watch was stopped and the time interval recorded.

On day 31 the animals were divided into two equal groups matched for activity level and running time based upon the records of the previous 10 days, and a test was conducted to determine the effects of TEA upon these two motor responses. In the experimental group, each of the six animals received the injection of TEA immediately prior to its daily 20-min. trial in the activity drum, of the same dosage employed in the lever-pressing experiment. Twenty minutes after injection, following completion of the activity-wheel run, each animal was placed in the starting box of the straightaway, and its running time in reaching the goal box was recorded. Exactly the same procedure was followed with the control animals using volumetrically equivalent injections of normal saline.

From experimental day 32 through day 41, all animals were again given daily recorded trials in both the activity wheel and the straightaway with no further injection. Again, on day 42, a test was conducted to determine the effects of TEA upon activity level and the running response. As in the lever-pressing experiment, the six animals which had served as controls on the first test were now injected with TEA, while the six former TEA animals now served as controls. On days 43, 44, and 45, all animals were again given daily trials in both the activity wheel and the straightaway to test recovery from the effects of the injections.

Results

The results of this second experiment are shown in Figures 1 and 2. It will be seen from Figure 1 that there is a significant drop (.01 level of confidence) in activity level for the TEA-injected animals on both test days. In addition, Figure 2 indicates that there was also a significant increase (.01 level of confidence) in running time on the straightaway for the TEA-injected animals on both test days.

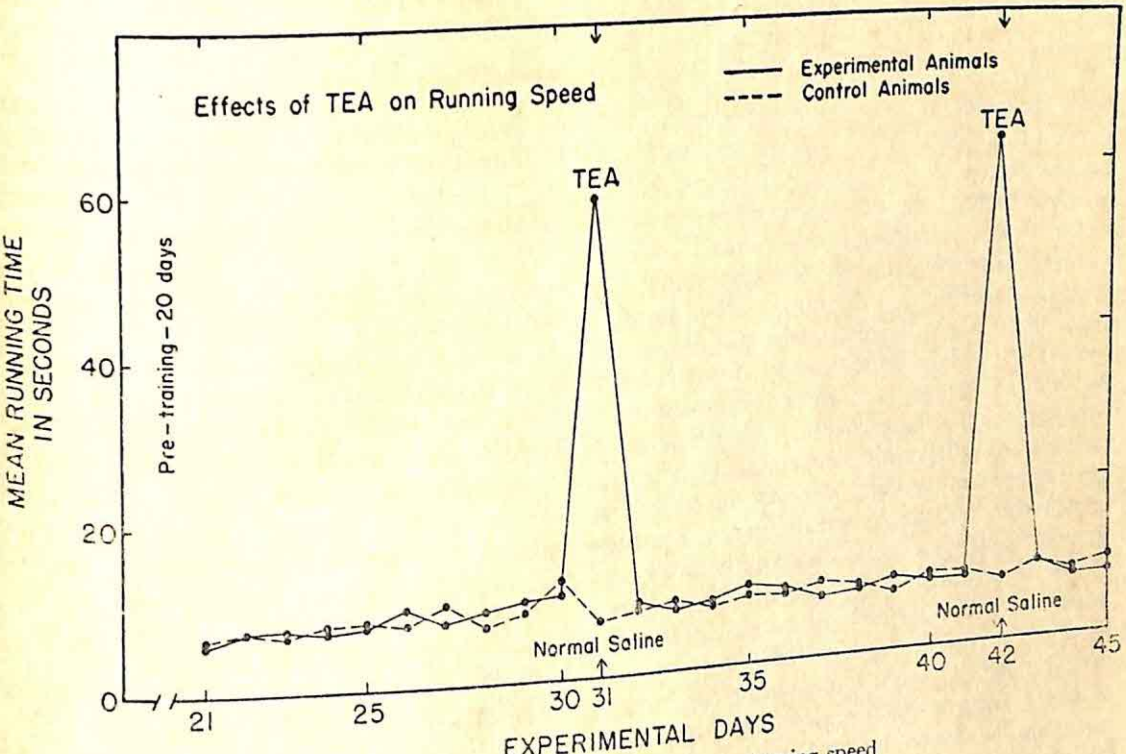

FIG. 2. The effect of tetraethylammonium on running speed

DISCUSSION AND CONCLUSIONS

The results of the present experiments indicate quite clearly that the effects of TEA upon the rat are probably considerably more general than those which could be accounted for by the presumed specific autonomic blocking at the ganglion. Pharmacologic studies by Birchall, Taylor, Lowenstein, and Page have demonstrated quite clearly that dosages of TEA (4 to 7 mg/kg of body weight), less than one-fourth as large as those used in Auld's experiment (31 mg/kg of body weight), can produce "generalized muscular weakness" in human patients such that "voluntary motion required much effort" (2, p. 575). The cumulative weight of both these independent lines of evidence would certainly seem to suggest that the action of the drug produces a rather marked effect upon locomotion and other motor capacities in the organism.

It might be argued, however, that the results of the present experiments are interpretable as indicating only that TEA reduces a number of other drives in addition to the fear drive, including activity, hunger, and thirst. Gross measurement of the amount of food and water consumed by the TEA-injected animals in the goal box of the runway as compared with the consumption level for the control animals under the same conditions, however, does not support such an interpretation. Although the experimental animals required a significantly longer period of time to navigate the 8-ft. runway, they showed no hesitation in gaining access to the food and water upon arrival in the goal box, and consumption during the 20-min. period during which they were allowed to remain in the goal box did not differ significantly from that of the controls under the same circumstances.

In the light of these data, Auld's interpretation of the depressing effects of TEA upon the speed of an escape response in terms of "fear reduction" would certainly appear rather tenuous, and his conclusion that the outcome of the experiments was "not [the result] of muscular weakness, in-coordination, or stupefaction" (1, p. 573) would hardly seem justified. Indeed, it would appear that any or all of these three possibilities would provide a far more parsimonious explanation than his "fear-reduction" interpretation.

SUMMARY

Two experiments have been performed to investigate further the reported fear-reducing properties of tetraethylammonium chloride (TEA) in rats.

1. In Experiment 1, a conditioned fear response was superimposed upon a previously established lever-pressing habit in 12 male albino rats. The depressing effects of TEA upon lever-pressing performance made it impossible to determine the effects of the drug upon the fear response and suggested that previously reported changes in behavior following administration of TEA might well be attributable to its effect upon the motor capacities of the organism.

2. In Experiment 2, the effect of TEA upon motor performance in an activity wheel and upon the speed of a hunger-and-thirst-motivated running response in rats was investigated. In both tests, significant depression of motor activity directly attributable to TEA was apparent.

3. The results of these experiments raise serious questions about the validity of previously published "fear-reduction" interpretations of TEA effects upon behavior.

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DECREASED AUTONOMIC FUNCTIONING AND EXTINCTION OF A CONDITIONED EMOTIONAL RESPONSE[1]

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Previous experimental studies have indicated that a conditioned emotional response is mediated, at least in part, by the autonomic nervous system. Solomon and Wynne (7) demonstrated that acquisition and retention of an avoidance response in dogs is altered by sympathectomy, and a recent experiment by Auld indicated that blocking the peripheral action of the autonomic nervous system in rats increases the latency of an avoidance response. Auld concluded that "the fear drive is at least partially dependent upon peripheral autonomic responses" (3, p. 573). The present research, based on a generalization of the results of these studies, is designed to investigate the effects of temporarily decreased autonomic functioning on the extinction of a conditioned emotional response in rats.

This study began with the assumption that intense peripheral action stimulated by the autonomic nervous system may be punishing and serve to inhibit the extinction of a conditioned emotional response. A typical conditioning procedure illustrates this theoretical sequence. Electric shock (US) is paired with presentation of a buzzer (CS); on subsequent trials only CS is presented to *S*, and a response of the autonomic nervous system is evoked. The autonomic discharge stimulates a diffuse pattern of peripheral activity evidenced by changes of blood pressure, heart rate, etc.; if there are relatively strong peripheral effects, CS is associated with an internal form of punishment, and extinction of the conditioned emotional response is inhibited.

From this theoretical formulation, it was deduced that temporarily blocking the autonomic nervous system should decrease the strength of a conditioned emotional response on subsequent trials in which the autonomic nervous system is physiologically normal.

In a situation previously associated with punishment and from which escape is prevented, rats exhibit a typical crouching or freezing pattern of behavior. This general inhibition of behavior in the rat is exhibited in a wide range of situations involving punishment and, presumably, is a conditioned emotional response. In the usual avoidance training procedures, for example, rats frequently show crouching or freezing behavior upon presentation of CS during the initial training trials. Miller has described the tendency of rats to remain motionless in response to fear as one of the "most obvious behavioral effects of fear" (6, p. 441). A measure of overt activity which is opposed to remaining motionless, therefore, offers a means of estimating the strength of a conditioned emotional response in the rat. In the present experiment, estimation of the strength of the conditioned emotional response was based on the assumption that general overt activity of the rat in a situation previously associated with punishment and from which escape is prevented is inversely related to the strength of the conditioned emotional response. In other words, the greater the activity of the rat in the experimental situation, the weaker the strength of the conditioned emotional response. Considering the initial theoretical postulate, it was predicted that temporarily blocking the autonomic nervous system would increase activity during subsequent trials in which the autonomic nervous system was normal.

METHOD

Subjects

The *S*s of this experiment were 30 albino rats bred in the psychology laboratories at the University of Illinois. There were 8 males and 7 females in each group. The animals were between 60 and 75 days old at the beginning of the experiment.

Apparatus and Measurement of Activity

The experimental apparatus consisted of an enclosed box with a grid floor which could be electrified. The dimensions of the box were 4.5 by 14 by 28 in. All

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[1] The writer wishes to express his appreciation to Professors J. McV. Hunt, O. H. Mowrer, and L. I. O'Kelly for their help throughout the present study. The writer also wishes to thank Professor J. Cohen for his help in the preparation of the manuscript.

[2] Ford Foundation Fellow.

walls were black, and the box was illuminated by two 7.5-w. bulbs. The animals were observed in a mirror placed below the grid floor and extending the full length of the box. The mirror was divided into five equal spaces, each 5.6 in. long. Activity was measured by counting the number of spaces traversed by the animal during each trial.

Blocking the Autonomic Nervous System

The peripheral action of the autonomic nervous system was blocked by administration of tetraethylammonium chloride (TEA), which temporarily blocks the transmission of impulses through the ganglia of both sympathetic and parasympathetic divisions of the autonomic nervous system. No major side effects have been discerned, except with very large doses, and no permanent physiological changes have been reported. Tolerance is apparently not developed on successive injections, and the drug is normally excreted within several hours after administration (1, 2, 4, 5). The administration of TEA followed the procedure outlined by Auld (3). A solution of 12.5 mg/cc concentration was used. The experimental animals received an intraperitoneal injection of 31 mg/kg of body weight, while the control animals received a volumetrically equivalent amount of physiologically normal saline solution.

Procedure

Training. On the first day of the experiment the animal was placed in the experimental apparatus for a 9-min. period. An electric shock of 150 v. through 175,000 ohms resistance was administered for 10 sec. after the animal had been in the apparatus for 3 min., and once again, after 6 min. The animal was returned to the home cage at the end of the 9-min. period. This procedure was repeated after an interval of 4 hr. There was no additional training. The experimental and control groups followed the same training procedure.

Extinction. Following training, the experimental procedure involved a series of 20 nonshock trials. Two trials were conducted daily for ten successive days after training. For the experimental group, the autonomic nervous system was blocked on alternate trials; for the control group, the autonomic nervous system was normal on all trials. The hypothesis was tested on the basis of activity during those intervening trials in which the autonomic nervous system was normal for both experimental and control groups. In terms of the activity of the autonomic nervous system, the series of 20 extinction trials for the experimental group followed the sequence: normal, blocked, normal, blocked, etc.; for the control group, on the other hand, the autonomic nervous system was normal on all 20 trials. The effects of temporary autonomic blockage were determined by comparing the activity of animals in the experimental group during those trials in which the autonomic nervous system was normal and the activity of animals in the control group on corresponding trials.

On the first trial of each day the animal was placed in the apparatus for 5 min., and the number of spaces traversed during this period was counted. For the first trial each day the procedure was identical for both experimental and control groups. Four hours after the first daily trial, the animals in the experimental group received an injection of TEA, while the animals in the control group received an equivalent injection of physiologically normal saline solution. Twenty minutes was allowed for the drug to take full effect; after 20 min. the animal was placed in the apparatus for a second 5-min. period.

The experimental group received 10 trials with the autonomic nervous system normal (the first trial of each day), and 10 trials with the peripheral action of the autonomic nervous system partially blocked (the second trial of each day). The control group received the total of 20 extinction trials with the autonomic nervous system normal. With the exception of the day after training, the first trial of each day provided the estimate of the dependent variable, viz., the amount of activity of experimental animals with the autonomic nervous system normal after one or more trials in which the autonomic nervous system had been blocked vs. the amount of activity of the control group in which the autonomic nervous system had been normal on all previous trials. If the 20 extinction trials are numbered consecutively, the odd-numbered trials, 3 through 19, can be designated *test trials*; according to the hypothesis, it was predicted that the experimental animals would evidence more activity than the control animals on these trials. The second trial of each day, the even-numbered trials, represents the independent variable, viz., encountering the situation previously associated with electric shock with the autonomic nervous system blocked vs. encountering this situation with the autonomic nervous system normal.

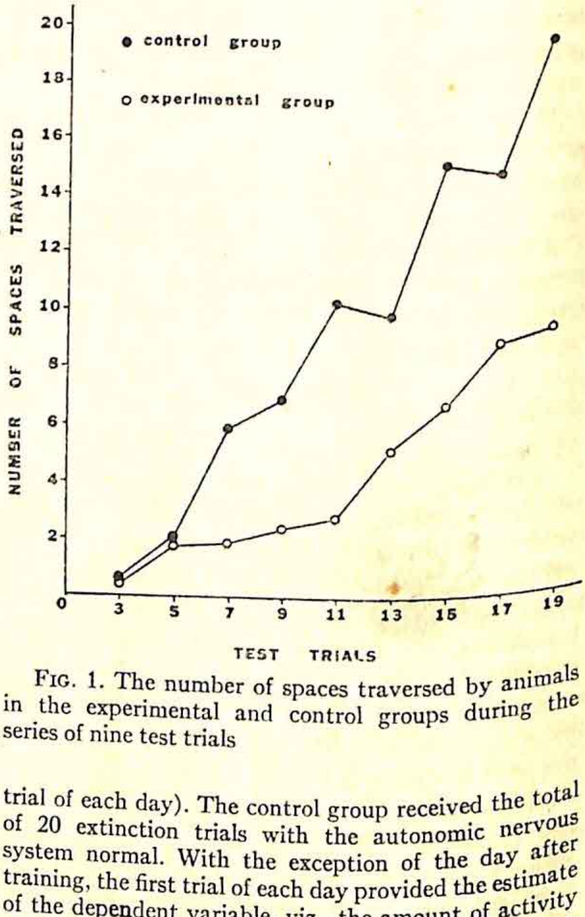

FIG. 1. The number of spaces traversed by animals in the experimental and control groups during the series of nine test trials

RESULTS AND DISCUSSION

Activity was measured in terms of the number of spaces traversed by a rat during each trial. An estimate of pretraining activity was derived empirically from an initial 3-min. period in the apparatus before the first electric shock was administered. The mean number of spaces traversed by the rats in the experimental group during this first 3-min. period was 33.2; for the rats in the control group, 31.4. The chances are greater than one in five that these two distributions could come from the same population, and the slight difference between means is not statistically significant.

It was predicted that the conditioned emotional response of animals in the experimental group would extinguish more rapidly than that of the control group, and that the experimental group, therefore, would show greater activity during the test trials. The data, summarized in Figure 1, clearly contradict the prediction. The mean number of spaces traversed during the total of nine test trials for the experimental group is 39.6, and for the control group, 86.7. It must be concluded, therefore, that, under the conditions of the present experiment, blocking the autonomic nervous system during part of the extinction trials *does not* increase activity nor decrease the conditioned emotional response on subsequent trials in which the autonomic nervous system is normal.

The control group consistently showed more activity than the experimental group during the test trials, and the difference in the means of the total number of spaces traversed during the test trials by rats in the two groups is statistically significant at the .05 level of confidence. The apparent direction of the effect suggests that blocking the autonomic nervous system on part of the extinction trials inhibits, rather than facilitates, the extinction of a conditioned emotional response on subsequent trials in which the autonomic nervous system is normal.

SUMMARY

It was predicted that temporarily blocking the autonomic nervous system would decrease a conditioned emotional response on subsequent trials in which the autonomic nervous system is normal. Two groups of albino rats were *S*s of the experiment, which involved administration of electric shock followed by 20 nonshock extinction trials. The autonomic nervous system of the experimental animals was blocked on alternating trials, and the strength of the conditioned emotional response, estimated by a measure of activity, was determined on the intervening trials in which the autonomic nervous system of both experimental and control animals was normal. The results clearly contradict the prediction, and it is concluded that temporarily blocking the autonomic nervous system does not decrease the conditioned emotional response when the autonomic nervous system is normal. The data suggest the hypothesis that temporary autonomic blockage inhibits, rather than facilitates, extinction of a conditioned emotional response.

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THE EFFECT OF THE HUNGER AND THIRST DRIVES UPON EXPLORATORY BEHAVIOR

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It is commonly assumed that amount of exploratory behavior is a positive function of strength of primary drive, e.g., hunger. From a biological standpoint such a relationship would possess survival value for an organism: when a primary drive arises, general activity increases. Hence the probability that a "successful" response, e.g., one leading to food, will occur also increases.

Certain observations made by the author during his investigations of exploratory behavior (3, 5) suggested that the above assumption may be false or, at best, oversimplified. For example, rats kept on a restricted diet for five days showed no increase in amount of exploratory behavior over rats allowed free access to food (3). Moreover, in several studies of adult female rats no evidence was found of marked cyclic changes in amount of exploratory behavior such as would occur if the estrus cycle were a determining factor.

The present paper reports two experimental tests of the above assumption.

EXPERIMENT I

Purpose

This experiment was designed to determine whether food or water deprivation affects either the amount or the orderliness of exploratory behavior.

Method

Subjects. The *S*s were 24 female albino rats of the Wistar strain. They were about 100 days old and had never been used in an experiment.

Apparatus. The apparatus consisted of an enclosed, symmetrical, single-unit Y maze constructed from ¾ unpainted white pine. Each arm was 24 in. long, 4 in. wide, and 4 in. high, and was covered with hardware cloth. The maze was placed in the center of an 8-ft. square enclosure formed by black curtains and illuminated by a single 40-w. bulb suspended 3 ft. above the choice point. To facilitate observation, each arm was marked off in 12-in. "units." The *E* observed the animals in the maze from behind the curtains.

Procedure. Eight rats were assigned at random to each of three groups, a hunger group (H), a thirst group (T), and a control group (C). The experiment lasted seven days. On days 1 through 7 group H was placed on a 7-gm. maintenance diet, group T was given access to water for 1 hr. per day, and group C was allowed free access to both food and water. On day 5 each rat was permitted to explore the Y maze freely for 5 min.; on days 6 and 7 each animal was exposed to the maze for 10 min. The *S*s were always placed in the maze at the choice point. For each animal on each day a record was made of the number of 12-in. units explored per minute and the order in which the units were explored. The criterion of a maze-unit exploration was a full body-length entry into a 12-in. unit. Neither food nor water was ever present in the maze. The animals in groups H and T were given their daily food or water ration at least ½ hr. after they were removed from the maze.

Results

Amount of exploratory behavior. Amount of exploratory behavior is measured by the number of 12-in. units explored. These data are summarized in Table 1 and in Figure 1. Inspection of the table reveals (*a*) that group C exhibited a *greater* amount of activity than either of the other two groups and (*b*) that there was little or no difference between groups H and T in amount of activity. Statistical analyses bear out these conclusions. The total number of 12-in. units explored by each rat was obtained for each day and for all three days combined. Four analyses of variance were run on these four sets of data. The between-group *F* ratios and their significance levels are presented in Table 1. Three of the four *F*'s are significant at the .05 level or better. A series of *t* tests shows that in no case is there a significant difference between groups H and T in average amount of exploratory behavior, and that group C exhibits a greater amount of activity than either of the other groups on days 2 and 3 and on all three days combined. Hence, food or water deprivation significantly reduces amount of exploratory behavior in a simple maze.

In Figure 1 mean amount of exploratory

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[1] These experiments were conducted in the Psychological Laboratory of Cornell University.

behavior is plotted as a function of time of exposure to the maze. The data for groups H and T are combined, and the data for days 2 and 3 are combined. Group H-T exhibits a lesser amount of activity than group C throughout the exposure period. The curves, however, are similar in shape. When the H-T curve is multiplied through by the constant 1.32, it is closely superimposed upon the curve for group C. Thus, food or water deprivation produces a general reduction in amount of exploratory behavior but does not change its relation to time of exposure to a simple maze.

TABLE 1

Mean Number of 12-In. Units Explored by Each Group on Each Day*

DAY	GROUP C	GROUP H	GROUP T	BETWEEN-GROUP *F*	*p*
1	53.1	44.2	44.2	1.81	—
	(12.4)	(5.4)	(12.5)		
2	84.9	63.2	67.6	5.47	.05
	(15.4)	(14.1)	(11.7)		
3	80.9	59.1	60.9	10.66	.001
	(13.6)	(7.2)	(10.2)		
Total	218.9	166.6	172.8	8.26	.01
	(37.6)	(20.3)	(23.3)		

* Values in parentheses represent the best estimate of the *SD* of the population.

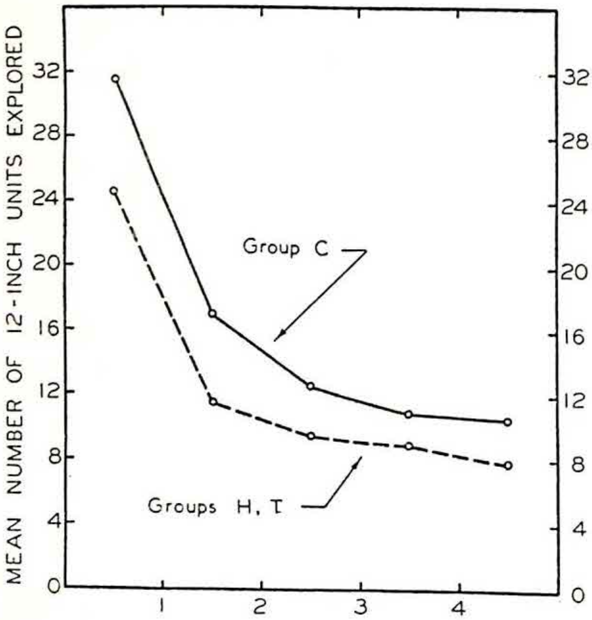

FIG. 1. Average amount of exploratory behavior as a function of time for the deprived and control groups

Orderliness in exploratory behavior. The number of times each animal entered three *unlike* arms in succession was tabulated for each day. The resulting values were averaged and converted into percentages for each group. The results are summarized in Table 2. No differences among groups are evident. Over the three days the average for all three groups is 68 per cent, a value far greater than the .001 fiducial limit based upon chance. This value compares very favorably with the 67 per cent obtained in an earlier study (3) in which rats were permitted to explore an elevated Y maze constructed from 30-in. arms. In brief, neither food nor water deprivation affects the orderliness of exploratory behavior in a simple maze.

TABLE 2

Percentage Choice of Three Successive Unlike Arms*, †

DAY	GROUP C		GROUP H		GROUP T		TOTAL	
	N	%	*N*	%	*N*	%	*N*	%
1	103	75.8	82	75.2	77	70.6	262	74.0
2	150	63.6	111	65.0	114	66.3	375	64.8
3	149	69.3	105	66.1	109	68.1	363	68.0
Total	402	68.6	298	67.9	300	68.0	1000	68.2

* *N* represents the total number of triads containing three unlike members.

† All percentages differ from chance at the .01 level or beyond.

EXPERIMENT II

Purpose

This experiment was designed (*a*) to provide a check on the results of Experiment I and (*b*) to obtain a first approximation to the functional relationship between length of food deprivation and amount of exploratory behavior.

Method

Subjects. The *S*s were 20 female albino rats of the Wistar strain. They were about 100 days old and had never been used in an experiment.

Apparatus. The apparatus was identical in every respect with that used in Experiment I.

Procedure. Ten rats were assigned at random to each of two groups, a hunger group (H) and a control group (C). Prior to the experiment all animals were allowed free access to food and water in their home cages at all times. This treatment was continued for group C throughout the experiment. The rats in group H, however, were given no food after being taken from their cages for their first maze exposure. On each of the four days of the experiment each animal was permitted to explore the Y maze freely for 10 min. Neither food nor water was ever present in the maze. The rats were always placed in the maze at the choice point, and their behavior was recorded in the same way as in Experiment I.

Results

Amount of exploratory behavior. These data are summarized in Table 3 and in Figure 2. Table 3 presents the mean number of 12-in. units explored by each group on each day and on days 2 to 4 combined. It also presents the *t* ratios and their levels of significance for all between-group comparisons. Inspection of the table reveals that on day 1 the groups did not differ in amount of exploratory behavior, but that on days 2, 3, and 4, and on days 2 to 4 combined, group H exhibited significantly less activity than group C. A series of *t* tests shows that both groups exhibit significantly less exploratory behavior on day 2 than on day 1 (.01 level), but that they show no further decrease. These results indicate that (*a*) 24-hr. food deprivation produces a significant decrement in amount of exploratory behavior, but that (*b*) 48- and 72-hr. deprivations produce no additional decrements.

TABLE 3

Mean Number of 12-In. Units Explored by Each Group on Each Day[*]

DAY	GROUP C	GROUP H	*t*	*p*
1	97.0 (10.1)	91.5 (24.8)	.65	—
2	81.4 (11.7)	63.9 (16.7)	2.65	.02
3	77.8 (12.6)	55.5 (16.1)	3.47	.01
4	77.0 (14.7)	56.1 (20.3)	2.64	.02
Days 2–4	236.2 (35.1)	175.5 (44.2)	3.40	.01

[*] Values in parentheses represent the best estimate of the *SD* of the population.

In Figure 2 average amount of exploratory behavior is plotted as a function of 2-min. periods of maze exposure for both groups. The data for days 2 to 4 are combined. The curves for the two groups are similar in shape, both decreasing in a regular manner, but the curve for group H is consistently below that for group C. If the curve for group H is multiplied through by the constant 1.36, it is closely superimposed upon the group C curve. This value is very close to the 1.32 found in Experiment I. In brief, food-deprivation periods of 24, 48, and 72 hr. produce an over-all reduction in amount of exploratory behavior but do not affect its relation to time of maze exposure.

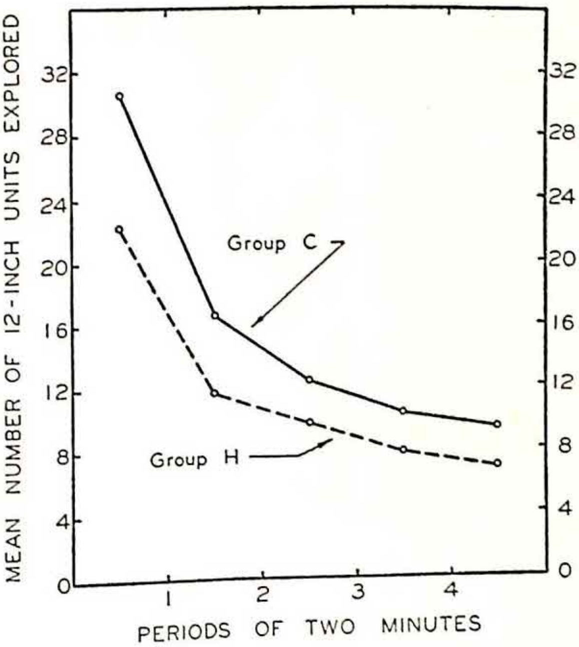

FIG. 2. Average amount of exploratory behavior as a function of time for the deprived and control groups on days 2 to 4

TABLE 4

Percentage Choice of Three Successive Unlike Arms[*]

DAY	GROUP C		GROUP H		TOTAL	
	N	%	*N*	%	*N*	%
1	226	68.3	207	68.8	433	68.5
2	174	63.1	123	58.9[**]	297	61.2
3	172	66.2	116	65.6	288	65.9
4	169	66.0	118	65.6	287	65.8
Total	741	66.0	564	65.1	1305	65.6

[*] *N* represents the total number of triads containing three unlike members.

[**] Significantly different from chance at the .02 level; all other percentages are significant beyond the .001 level.

Orderliness in exploratory behavior. These results are summarized in Table 4, which presents the total number of three-unlike-arm triads for each group on each day and for all days combined. The corresponding percentages are also given. Inspection of the table reveals that there are no appreciable differences between groups on any one day or on all days combined. All percentages differ from chance at the .02 level or beyond. The combined average for both groups over the four days is 66 per cent, a value in close agreement with the 68 per cent obtained in Experiment I. To summarize: food-deprivation periods of 24, 48, and 72 hr. produce no changes in the order characteristics of exploratory behavior in a simple maze.

DISCUSSION

The major findings of these two experiments are: (1) 24-hr. food or water deprivation (*a*) significantly reduces amount of exploratory behavior but (*b*) does not affect its orderliness; and (2) 48- and 72-hr. food deprivations (*a*) produce no further reduction in amount of exploratory behavior and (*b*) do not change its order characteristics.

Results 1*a* and 2*a* contradict the common assumption that exploratory behavior increases in amount when a primary drive arises. Two possible explanations of this finding will be considered. First, it is possible that food or water deprivation strengthens certain behaviors that are incompatible with the kind of exploratory behavior measured in these experiments. Hence locomotor activity is reduced because of competing behaviors such as sniffing or chewing on maze corners. Although no quantitative data were recorded, *E* detected no differences among groups in either kind or incidence of behaviors. Furthermore, this hypothesis implies that the hunger and thirst groups differ in kinds of competing responses. Thus, they might be expected to differ in amount of reduction of exploratory behavior. Such a difference did not occur. It also leads to the prediction that, because the frequency or strength of competing responses should increase with strength of hunger drive, the amount of reduction in exploratory behavior should increase with length of deprivation. The results of Experiment II do not confirm this prediction. Therefore, although it is not disproved, this hypothesis is not supported by available observations.

The second explanation concerns drive interaction. This kind of phenomenon is not unknown. For example, it is well known that an animal which is both hungry and thirsty eats less than an animal which is hungry only. It is hypothesized that the presence of a primary drive such as hunger reduces the strength of the exploratory drive evoked by a novel situation. Thus, less exploratory behavior occurs in that situation. The present results are in agreement with this hypothesis: in all deprived groups amount of exploratory behavior began at a level less than that of the controls and decreased in a regular manner.

If exploratory behavior is viewed as general activity, there is an apparent contradiction between the present results and those reported by certain other investigators. Studies in which activity cages are used yield greater amounts of general activity when such drives as hunger, thirst, and sex are present than when they are absent (e.g., 1, 6). However, the procedure employed in such studies differs in one important respect from that used in the present experiments. Instead of being exposed to a novel environment for a limited time each day, the *S*s are either permitted to live in an activity cage or are given free access to one at all times. Under the latter conditions it is probable that the strength of the exploratory drive aroused by the cage rapidly decreases to and remains at a low level. Therefore, the measurements reported reflect the effect of these drives upon general activity in the absence of any appreciable degree of strength of the exploratory drive, i.e., they are not indices of exploratory behavior per se.

This consideration makes it possible to resolve the apparent contradiction stated above. The exploratory drive is a primary motive, largely but not wholly independent of other primary drives. When it exists in a high state of strength it exerts a dominant influence on behavior, even when other primary drives are present. Because the maze was a novel environment for all animals in the present experiments, it aroused a strong exploratory drive that in turn produced exploratory behavior, not "general activity." The statement that the exploratory drive, when strong, predominates over other primary drives is supported by numerous observations of the author that even very hungry or thirsty rats will not eat or drink in a novel environment until they have explored it.

Results *1b* and *2b* indicate that a hungry or a thirsty rat is neither more nor less "systematic" in exploring a novel environment than a satiated rat. (However, this does not imply that previously established behavior patterns of "searching," e.g., for food, are not evoked by relatively novel environments, i.e., that stimulus generalization will not be operative.) These results support previous evidence (2, 3, 4, 5) that exploratory behavior of the kind studied in these experiments is largely under the control of external stimuli. They also support the statement made above that the exploratory drive is a primary drive, largely independent of other primary drives: although amount of exploratory behavior decreased under food and water deprivation, no change in its orderliness occurred. Moreover, these results favor the second, but not the first, of the two hypotheses presented above. (*a*) If the presence of a drive such as hunger strengthens behaviors that compete with exploratory behavior, then the order characteristics of the latter should be changed, and the magnitude of the change should vary with length of deprivation. Neither prediction is confirmed. (*b*) If the presence of another primary drive simply reduces the strength of the exploratory drive, then the orderliness of exploratory behavior should remain unchanged. This expectation is confirmed by the results of both experiments.

No explanation is offered for the finding that food deprivation beyond 24 hr. produces no additional decrement in amount of exploratory behavior. Presumably the relation sought occurs between zero and 24 hr. of deprivation for the rat.

It should be pointed out that the two characteristics of exploratory behavior found in these experiments—an over-all decrease in amount and no change in orderliness under states of deprivation—possess survival value for an organism. It is to a deprived organism's advantage that it (*a*) conserve its bodily resources while exploring a novel environment which may or may not contain a commodity relevant to its existing need and (*b*) explore that environment thoroughly.

SUMMARY

Two experiments are reported in which the exploratory behavior of satiated and variously deprived rats was studied in a simple Y maze. The major findings are that food or water deprivation (*a*) significantly *reduces* amount of exploratory behavior, the maximal decrement occurring by 24 hr. for food deprivation, and (*b*) does not affect the orderliness of exploratory behavior. These results are interpreted as providing evidence that the exploratory drive is a primary drive, aroused by external stimuli, which undergoes a decrement in strength when another primary drive is present. It is concluded that the commonly held assumption that amount of exploratory behavior is a positive function of the strength of such primary drives as hunger and thirst is an oversimplification; the conditions determining the strength of the exploratory drive must be taken into account.

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RELATION OF RANDOM ACTIVITY TO FOOD DEPRIVATION

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It is usually taken for granted in textbooks of general psychology that increased "drive" produces increased random activity. For example, Dashiell says in his latest revision of his general text: "The unbalanced state [hunger] drives the organism into activity, and the activity continues until a steady state is restored" (2, p. 141).

It is also commonly assumed that the mechanism by which a drive state increases activity is a strong external or internal stimulus. Thus, pain from external shock has been treated as a typical drive state (3, 4), and activity produced by hunger has been treated as a response to a strong internal stimulus (6).

An alternative mechanism is that drives involve lowered thresholds to external stimulation. This hypothesis would predict little change in activity in an animal in a drive state unless there were some external stimulation. According to this hypothesis the drive state does not force activity; it merely makes the animal more responsive to environmental changes. Previous studies relating hunger drive to activity (e.g., 5, 7) have not made a specific attempt to maintain a constant environment. The main purpose of the present experiment was to compare the random activity of hungry animals before and after a marked environmental change. A second purpose was to relate this comparison to degree of deprivation. A third purpose was to check the hypothesis that drive activity is mediated by an increase in stimulation.

METHOD

The *S*s were 12 mature Wistar rats with a weight range from 310 to 410 gm. at the outset of the experiment. The activity measure used was worked out after a good deal of trial and error on a variety of devices for recording activity. The unit finally used has been described elsewhere (1). It consists of a round cage with four sensitive microswitches placed at each of the four quadrants. It is pivoted at the center and has about ⅛-in. clearance in tipping in any direction. It is wired so that any shift in the location of the "tilt" among the four quadrants will advance an electromagnetic counter. The apparatus usually fails to record certain small movements like scratching, but it records larger movements such as moving from one quadrant to another or shaking the cage.

Six of these units were installed in a cabinet soundproofed with Celutex. The cabinet was well ventilated by an exhaust fan, which also dominated the auditory field of the rat. To make doubly sure that auditory stimuli outside the cabinet would not affect *S*s, the cabinet was placed in a soundproofed room for the duration of the experiment. The auditory field could be varied by turning off the exhaust fan; the visual field could be controlled by turning on lights inside the two chambers of the cabinet, which were otherwise unlighted.

The animals were put into the cabinet and fed dry Purina pellets ad libitum for four days. They were then starved for three days. At a fixed time (noon) on each of the seven days their activity as recorded by the counters was measured for 10 min., after which an environmental change was introduced and their activity was recorded for another 10 min. The environmental change was both auditory and visual. The continual hum of the exhaust fan in the cabinet was turned off, and the lights in the cabinet were turned on. It should be further noted that the counters recorded—as a base line—the activity of the animals over every 24 hr., exclusive of the two 10-min. tests each day.

RESULTS AND DISCUSSION

The main results are shown in Figure 1. It can be seen that environmental change has a large effect on the random activity of *S*s. When the fan went off and the lights came on, *S*s became more active. This was true whether *S*s were satiated as in the first four days or whether they were hungry as in the second three days. This general difference is shown by the high level of the dotted line as contrasted with the solid line. The latter curve shows the mean number of counts per hour in the 10-min. tests before the environmental change. The solid line varies somewhat but seems to hold to a fixed level. The difference is well beyond the .01 level.

It can also be noted in Figure 1 that *S*s show a tendency toward adaptation to the environmental change during the satiation period. They reduced their activity somewhat by the end of four days of adaptation to the cages and the environmental change. But when they are deprived of food, they reverse the adaptation process and show a significant rise in activity in response to an external change as hours of deprivation are increased. The figure shows no noticeable trend toward an increase during the tests given just before the environmental change, even though the animals were starved over three successive days. These results support the idea that hunger drive involves a lowering of thresholds rather than an internal drive stimulus.

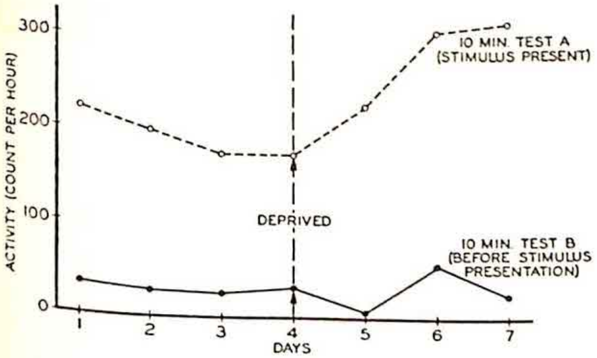

FIG. 1. The effect of deprivation on the activity response to an environmental change

To facilitate comparison of 10-min. test period activity and total daily activity, the data in Figures 1 and 2 are plotted in terms of counts per hour. To obtain this measure the activity scores for the 10-min. test periods were multiplied by six and the 24-hr. scores were divided by 24.

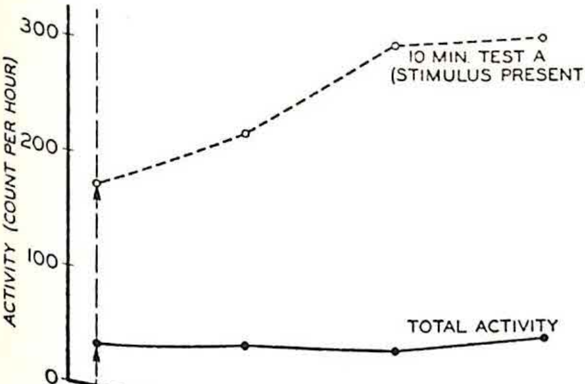

FIG. 2. A comparison of the effects of deprivation on "spontaneous" activity and the activity response to an environmental change

A logical implication of this interpretation is that animals should show increased activity with deprivation simply because they are always getting at least some external stimulation. They can feel their own responses, hear their own microswitches whenever they click, and hear the clicking of microswitches of the other two animals in their section of the apparatus. These stimuli should combine to produce an effect similar to the controlled environmental change of fan off and lights on as sources of stimulation producing an increase in activity due to lowered thresholds.

No significant rise was found in the 10-min. "before" tests, but they are not as reliable as the total activity through the 24 hr. of the three-day starvation period. If total activity over successive 24-hr. periods is plotted, a slight but statistically significant rise is found. This is shown by the solid line in Figure 2, and is compared with the effects of the controlled environmental change. The figure shows some increase in activity without any controlled change. The level of activity is much higher with the environmental change, however, and while both go up with deprivation, the increase is much more prominent in the case of a controlled environmental change.

SUMMARY

Random activity of 12 rats was measured for a period of seven days in a constant environment. During the first four days the animals were on an ad libitum diet; during the last three days they were deprived of all food. Activity was automatically recorded over each 24-hr. period. It was also recorded for 10-min. periods before and during a gross change in the auditory and visual environment.

It was found that: (*a*) an environmental change consistently produced an increase in activity; (*b*) without the environmental change there was a relatively small increase in activity with deprivation whereas there was a relatively large increase with deprivation during the environmental change.

The main conclusion is that hunger drive seems to involve lowered thresholds of response rather than internal stimulation to activity. The slight rise in general activity as the animals are starved over a three-day period is interpreted as due to their greater sensitivity to minimal stimulus changes in the environment provided. This rise was small relative to the rise in the effects of a large environmental change during the same starvation period. Starvation does not instigate activity;

it only lowers the threshold for normal stimuli to activity.

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EXPLORATORY BEHAVIOR AS A FUNCTION OF HUNGER IN "BRIGHT" AND "DULL" RATS[1]

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The experiment was carried out for two purposes. The first stemmed from the work of Berlyne (1) and Montgomery (2, 3, 4) on curiosity and exploration. These investigators found that rats tend to explore in a systematic manner an unfamiliar place or object, and that the amount of attention given by the animals decreases as a function of time. Berlyne (1) has given his results a Hullian treatment, postulating curiosity as a drive which is reduced under the perceptual stimulation arising from exploratory activity. By virtue of this need reduction, learning occurs. Montgomery's experiments, while giving some support to this interpretation, also tend to contradict it by showing that over five days of testing the amount of exploration shown each day by an animal tends to remain constant, rather than to decline, as one might expect from Berlyne's postulates. The two authors used different procedures, however, for measuring exploratory behavior. Montgomery's method involved a much greater component of sheer motor activity than Berlyne's.

Subsequently, Montgomery (4) examined the effect of food and water deprivation on exploratory activity. He found that under such conditions (five to seven days of reduced rations), rats explored not more but less than control animals not deprived. Orderliness of exploration remained unchanged. This reduction gave support to Montgomery's hypothesis that "the presence of a primary drive such as hunger reduces the strength of the exploratory drive evoked by a novel situation" (personal communication). However, he also deduced that this might not necessarily hold in a highly complex and novel situation where hungry or thirsty animals might explore more rather than less.

The present experiment attempts to check the effect of food deprivation on the amount and quality of exploration with groups deprived completely for relatively short periods and tested on a maze different from the mazes used by Montgomery.

The second purpose of the experiment was to discover if any differences in exploratory behavior could be shown between "maze-bright" and "maze-dull" rats. At McGill University, two such strains have been bred selectively on the basis of performance in the Hebb-Williams maze. At the fifth generation, overlap between the two lines was found to be almost completely eliminated, there being only one exception. In order to try to avoid the difficulty of having differences between the strains in traits other than the one on which selection was made (cf. Searle, 6), the preceding generation was tested on several simple measures of motivation and emotion. Selection was then carried on so as to randomize differences in these characteristics, as well as in body weight, while at the same time maximizing differences in the relevant trait (7). In these tests, as well as on the maze itself, there was some indication that there might be a difference in exploratory drive between the McGill bright and dull animals. Consequently, it was decided that this possibility could well be examined coincidentally with the problem outlined above.

METHOD

Animals

Twenty-eight "bright" (11 males, 17 females) and 32 "dull" (14 males, 18 females) rats of the McGill strain were used. All were experimentally naive and between 70 and 80 days of age. All were in good health.

Apparatus

An elevated maze was used. It was in the shape of a rectangle 15 in. by 30 in., divided in the center so as to give seven units, each 15 in. in length and 3½ in. wide. The pathway was 3 ft. from the floor. The whole maze was painted a flat black. Uniformity of surround was supplied by curtains of black cloth enclosing the maze on the sides and top. Lighting, from the neon overhead lights in the experimental room, was low and diffuse

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[1] This research was supported by grants from the National Research Council of Canada and the Rockefeller Foundation.

inside the cloth enclosure. A small hole was cut in one side of the curtain to permit observation by *E*.

Procedure

Each rat was assigned at random to one of three food-deprivation groups, 0-, 24-, and 48-hr. deprivation, with 20 rats per group. Each group could be further subdivided according to brightness and sex. In the 0-hr. group there were 10 bright (4 male, 6 female) and 10 dull (4 male, 6 female) rats; in the 24-hr. group, there were 8 bright (3 male, 5 female) and 12 dull (6 male, 6 female) rats; and in the 48-hr. group, there were 10 bright (4 male, 6 female) and 10 dull (4 male, 6 female) animals. At the start of each test, an animal was inserted in the enclosure at the starting point of the maze (where the center unit met one of the long sides) and allowed to explore freely for one 600-sec. session. The latter was divided, after Montgomery (2), into six 100-sec. periods, and the animal's path was traced during each of these. The testing was conducted at approximately the same time of day for all *S*s in order to insure uniformity of lighting conditions. A month later, all animals were tested on the Hebb-Williams open-field maze.

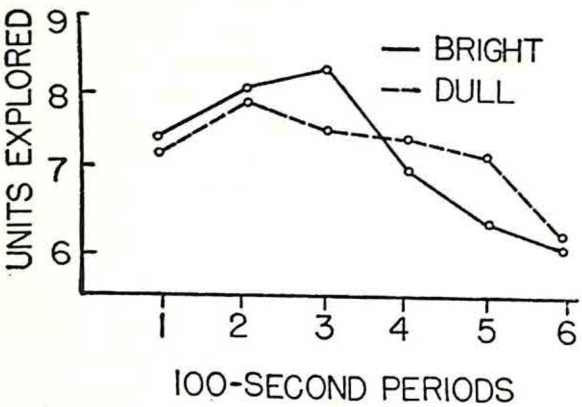

FIG. 1. Exploratory activity in "bright" and "dull" rats as a function of time

RESULTS

The exploration curves for McGill bright and dull animals are presented in Figure 1. Unlike Montgomery's curves (2), they decline only slightly over the 600 sec. of testing. The bright animals explored rather more than the dull during the first 300 sec., and less during the last 300 sec. However, these differences are not statistically significant. Within the bright and dull male subgroups, there did appear a tendency for maze ability and exploratory activity to correlate positively. The correlations were 0.53 for bright and 0.68 for dull. Only the second of these is significant. No relationship at all appeared in the female groups.

Table 1 shows the mean number of units traversed by male and female rats in each deprivation group. An analysis of variance computed on these data yielded a clearly significant difference between males and females ($F = 13.48, p < .001$), but none between the three deprivation groups. However, the interaction between sex and food deprivation was significant ($F = 4.35, p < .05$). Apparently males and females reacted differently under different degrees of hunger, a fact which is evident from inspection of Table 1. Males showed steadily increasing activity with increasing amounts of deprivation, but the greatest difference, that between the 0-hr. group and the 48-hr. group, in mean amounts of exploratory activity is not significant ($t = 1.76, p < .10$). Females showed a slight increase at first with 24-hr. deprivation, and then a sharp decrease with 48-hr. deprivation. The difference between the last two deprivation groups is significant ($t = 2.73, p < .01$). Because of the rise shown by males and the decline shown by females after 48-hr. hunger, there was no sex difference in exploratory activity at this point.

TABLE 1

Mean Number of Units Explored in a Seven-Unit Maze by Male and Female Rats under Three Degrees of Hunger

SEX	*N*	HOURS FOOD DEPRIVATION		
		0	24	48
Male	25	33.9	38.8	40.8
Female	35	47.6	51.1	40.2

The data were finally examined for differences between groups in the quality rather than the quantity of exploration. In general, all units of the maze received some attention during the 600-sec. test sessions, but the two units on either side of the starting point were explored more, and the center unit bisecting the maze was explored less than other units. These differences are, in fact, significant (chi square $= 10.21, p < .01$), and they are shown more or less equally by all groups. Each animal traversed each unit of the maze a certain number of times. The variance of the entries into each of the five units was computed for each animal, and an analysis of variance was calculated on these variances to test for the significance of differences between food-deprivation and maze-ability subgroups. Since no significant differences appeared, we can conclude that all animals traversed the maze in roughly the same manner, favoring the units near the starting point, but avoiding the center unit.

As in Montgomery's experiment, here, also, there was a tendency for animals to avoid a path traversed immediately before. On the basis of chance alone, we might expect as many repetitive (e.g., AA) as nonrepetitive (e.g., AB) two-unit sequences. The data show, for all rats, an average of 7.0 repetitive and 41.7 nonrepetitive sequences in the 600-sec. experimental period. The difference between these frequencies is significant (chi square = 24.08, $p < .001$). However, a comparison of the number of repetitive versus nonrepetitive three-unit sequences (e.g., ABB as against ABC) yields no significant difference, the means being 6.9 repetitive and 7.3 nonrepetitive triads.

In view of the nature of the maze used in the experiment and the unit preferences indicated previously, no attempt was made to analyze right- and left-going tendencies.

DISCUSSION

In general, the main results support Montgomery's data and verify Berlyne's Postulate II. Exploratory activity of rats declines with time of exposure to a particular place. There is little evidence that it is carried on in a very systematic manner.

The decline shown by the animals in this experiment was much less sharp than that found by Montgomery. This discrepancy may have depended on differences in the strains of animals, but it is more likely that it depended on differences in the mazes used. Since there was a tendency for the rats to avoid the center unit, the maze used in the present experiment was in a sense simpler than the T and L mazes employed by Montgomery. Further, since the pathway was continuous, and there were no corners or blind alleys in which an animal could crouch, forward-going tendencies may have been constantly encouraged, even at the end of a test session.

While no differences between bright and dull rats in exploratory activity were found, a clear sex difference did appear. Female animals explored significantly more than males. This result agrees with the fact that female rats show more general activity than males (5). Further, with increasing hunger, the amount of exploratory activity shown by females increased at first and then declined, while that of males tended to increase, so that under conditions of 48-hr. deprivation the difference between them was minimal. Since Montgomery (4) used only female animals in his experiment, these results are not in contradiction with his, but they do indicate that it is apparently not possible to generalize his results to males. The two sexes behaved rather differently in the present experiment.

This finding is not too easily explained. It is known that hunger increases general activity (5), and this may well relate to the increase in exploratory behavior shown by male rats. But the decrease shown by females still poses a problem. Perhaps a clue to its solution may be gained from some of the Columbia obstruction studies. In one experiment Warner (8) found that male rats crossed the grid a maximum number of times after four days of food deprivation, while females crossed most after only two or three days. If this means that under hunger conditions a maximum activity level is reached sooner by females than by males, it is in line with the present results. Thus female rats showed an increase in exploratory activity after 24-hr. food deprivation and a sharp decrease after 48 hr., while males showed a steady increase up to 48 hr.

Whatever the explanation, such a result suggests a need for caution in formulating general laws of behavior. Sometimes differences in genetic constitution (as between the sexes) may be great enough to produce gross differences at the behavioral level. If these are not taken into account and specified, the value of any broad postulates set up may be seriously reduced.

SUMMARY

The experiment was designed to examine two main problems: (*a*) the effect of hunger on exploratory activity and (*b*) the relation between maze brightness and exploratory activity. Sixty hooded rats, 28 McGill "bright" (11 males, 17 females) and 32 McGill "dull" (14 males, 18 females), were used in the experiment. They were divided randomly into

three food-deprivation groups, 0-, 24-, and 48-hr. deprivation. All were run on a seven-unit elevated maze for one 600-sec. test session. The path of each animal was traced and the number of units traversed per 100-sec. period was used as a basis for comparing the groups. The results justified the following conclusions:

1. Exploratory activity in a restricted unfamiliar situation declines as a function of time.

2. Food deprivation increases exploratory activity in male rats, but decreases it after a certain point in female animals.

3. Maze brightness is not related to exploratory activity as measured.

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EATING AND DRINKING AS A FUNCTION OF MAINTENANCE SCHEDULE

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Animals without water do not eat as much food as usual, and hungry animals do not drink much water (4, 8, 13, 16, 17, 20). Animals drink more after meals than at other times. The dog and hen (13) and the rat (20) show a drop in food intake during water deprivation. Dogs (5, 11) and rats (20) similarly drop in water intake during food deprivation. Rats drink more after a period of water deprivation during which food is available than after a similar period with no food available (17). The corresponding case for food intake apparently has not been investigated. After protracted periods of food or water deprivation, rats exceed in both drinking and eating their average value before deprivation (4).

No systematic sets of data are available on these phenomena as they are encountered in studies of learning, although their significance for theoretical formulations of "motivation" and learning has not escaped some investigators (9, p. 234; 22). Recent studies on "drive interaction," "drive discrimination," and on "cognitions" have involved the control of the behavior of food-deprived and of water-deprived rats by food and water placed in goal boxes and alleys (21). These have not had uniform results, so that it is pertinent to examine the matter more closely.

Today's learning theorists are in fair agreement on a definition of "drive." This concept is an intervening variable, explicitly involving two sets of operations and implicitly a third.[2] The first operations establish drives; e.g., for hunger and thirst, the animal is deprived of food and water, respectively, for a stated number of hours. The second class of operations is the measurement of classes of behavior (running, bar pressing, eating) that vary with the duration of the preceding deprivation. The third, implicit, operation is that of satiation, usually giving the animal access to food and water long enough so that it neither eats nor drinks for a specified period. "Satiation" operations vary considerably.

In this experiment, the operations are depriving the animal of food or water, or both, through stated intervals of time following free feeding and free drinking. The measure of behavior chosen is the total weight, in grams, of food and water ingested by the animal in the first hour following the period of deprivation. The adequacy of these measures has been established by others (1, p. 128; 2, 7, 15, 18, 19).

The general plan of the experiment and the values of the variables investigated have been chosen to provide data useful for the interpretation of experimental data in the field of learning.

EXPERIMENT I

Method

Subjects. Twelve male albino rats (Hisaw strain) ranging in age from 97 to 100 days at the beginning of the first experiment were the *S*s. Before the experiment, they were caged in groups of six, with continuous access to food and water.

Experimental room and apparatus. The rats lived in a small internal room, with one door (closed) and no window. An automatic timer turned on two fluorescent ceiling fixtures at 1900 daily; they were turned off at approximately 0700. A heater was turned on by a thermostat when the room temperature fell to 65° F; no attempt was made to control humidity. A continuous, 24-hr. record showed that the mean temperature throughout the experiment was 70.8° F with a range from 63.3° F to 75.5° F; the mean relative humidity was 50.0 per cent with a range from 39.5 per cent to 62.8 per cent.

Each animal lived separately in an 11-in. by 8-in. by 8-in. wire-mesh open-bottom cage resting on a wire-mesh grating mounted on a metal rack. A paper-lined tray under each cage caught feces and food particles that fell through the mesh. No attempt was made to control coprophagia.

Measurements. Weighed rations of food, greater than the amount the animal could eat, were placed in each cage at the beginning of the period. At the end of the period, the food remaining was taken from the cages. Food particles were carefully collected from the trays, dried, and added to the food taken from the cages, and the whole then weighed. The difference between the initial amount and the amount recovered was taken as the measure of food eaten. The error of measurement in this operation was approximately .05 gm.

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[1] Now at the Massachusetts Institute of Technology.

[2] Hull's 1943 theory of drive (9) is in somewhat different status. Laws relating *D* to privation and other experimental variables are not incorporated in the theory, but are left stated somewhat casually (e.g., $D = f(h)$) in the supporting text. The details of these relationships were left open, presumably to be filled in empirically.

An inverted, rubber-stoppered, 250-cc. chemical graduate was mounted on the side of each cage. A short length of copper tubing led from the stopper through the side of the cage. The amount of water, to the nearest .5 cc., removed by the animal was determined by reading changes of water level from the calibrated graduate. A water bottle fitted to an empty cage yielded corrections for losses due to dripping and evaporation. This measure was converted into grams.

The experimental diet consisted of dry Purina Laboratory Chow biscuits and tap water. A small piece of fresh lettuce was given daily during the free-feeding period as a dietary supplement.

Preliminary handling. For 17 days prior to the beginning of the experiment, the animals were kept on a 24-hr. feeding schedule. At 2200 daily, they were given food and water. At 2000 on the following day, food and water were withdrawn.

Daily schedules. The experiment was performed in 12 experimental periods of six days each. The first five days of each period were experimental ones; the sixth was a recovery day, during which the animals had unrestricted access to food and water. Each experimental day began at 2200. From 2200 to 1900 of the following day the animals underwent a 21-hr. *deprivation period.* At 1900, food and water ingestion through this period were measured. Then followed a *measurement period* extending from 1930 to 2030. At 2030, food and water ingestion were again measured. At 2045 all animals were given free access to food (including the lettuce) and water, and the trays were changed. Shortly before 2200, food and water were removed and clean trays placed under the cages. The deprivation period of the new experimental day began at 2200, when the experimental rations were given. Each day, then, incorporated a 21-hr. deprivation period, a second deprivation period of ½ hr., and a 1-hr. measurement period. The remaining time was devoted to experimental routine and to free feeding and drinking.

On the fifth experimental day of each of the 12 experimental periods, from 2200 to 2130 of the next calendar day, all animals had free access to both food and water. Food and water were then removed, and at 2200 the new experimental period began.

Experimental treatments. Through all five deprivation periods of each experimental period, any of four different treatments could obtain. The rat might be given: (*a*) food and water (FW), (*b*) food but no water (F), (*c*) water but no food (W), (*d*) neither food nor water (0). These, together with the immediately following ½-hr. period with neither food nor water, establish four deprivation conditions: (*a*) FW—½-hr. food deprivation, ½-hr. water deprivation; (*b*) F—½-hr. food deprivation, 21 ½-hr. water deprivation; (*c*) W—21 ½-hr. food deprivation, ½-hr. water deprivation; (*d*) 0—21 ½-hr. food deprivation, 21 ½-hr. water deprivation.

During the 1-hr. measurement period the animals could be given (*a*) both food and water (fw), (*b*) food but no water (f), (*c*) water but no food (w).[3]

Measurements of both food and water ingestion were made at the end of both deprivation and measurement periods.

If we take all combinations of the two periods, there are 12 different experimental treatments of deprivation and measurement. Each rat underwent all 12. The order in which any one animal went through them was determined by picking cards from a hat. The experiment was performed through the period February 8 to April 21, 1951.

Results

Means of both food and water ingestion were computed for each treatment for the first two and for the last three days. Despite a slight tendency for intakes to be lower on the last three days, no significant differences appeared. For this reason, the data presented are the arithmetic means,[4] for each rat, of daily food and water intake over all five days of each experimental period.

Deprivation period. Table 1 presents the number of grams of food (1*a*) and water (1*b*) ingested by the animals during each of the three kinds of deprivation periods, subdivided according to the associated measurement periods. In Table 1 two-tailed matched t tests of the differences show that the differences between columns are significant at better than the .001 level in all cases, and that the differences within columns are not significant except for the greatest difference in the right-hand column of Table 1*a*, which falls between the .02 and .05 levels of probability; this may be expected by chance when 24 comparisons are made. Ingestion during the deprivation period did not depend on the measurement period of the preceding day. The data in each column were therefore lumped. In the 21-hr. period, the animals ingested approximately 51 gm. of substance when both food and water were available, 39 per cent of which was dry Purina Chow. This may be compared with Strominger's 33 per cent (20).

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[3] In specifying the experimental treatments, the notation introduced above will be followed throughout. When we refer to the *amounts* of food eaten, or water drunk, at any stage of the treatment, this notation will be extended by the use of italics. Thus FWfw refers to the treatment, whereas FW*fw* refers to the quantity of water drunk during the 1-hr. period when food is present, following a ½-hr. period of deprivation of both food and water.

[4] A log transform was not found to be necessary.

When food-deprived, the rats drank .41 as much as when food was available, and when water-deprived, they ate .57 of their normal intake. These numbers are the *W*/F*W* and *F*/*FW* ratios, respectively. Under these conditions the foodless animal limits its intake of water, and the waterless animal reduces the amount of food it eats. Water consumption is reduced more in this way than is food consumption.

TABLE 1

Experiment I

Food and Water Consumption during Deprivation Periods

(*a*) Food Consumption (gms.) during 21-hour Deprivation Periods as a Function of Associated Measurement Period*

ASSOCIATED MEASUREMENT PERIOD	DEPRIVATION PERIOD				*F/FW*
	F		*FW*		
	Mean	*SD*	Mean	*SD*	
f	11.81	1.83	20.34	2.54	.58
w	10.83	1.40	20.39	2.56	.53
fw	10.75	1.65	18.27	3.40	.59
Mean	11.13	1.63	19.66	2.86	.57

(*b*) Water Consumption (gms.) during 21-hour Deprivation Periods as a Function of Associated Measurement Period*

ASSOCIATED MEASUREMENT PERIOD	DEPRIVATION PERIOD				*W*/F*W*
	W		F*W*		
	Mean	*SD*	Mean	*SD*	
f	14.61	5.86	31.71	4.10	.44
w	12.92	5.96	32.97	7.05	.39
fw	11.29	5.38	29.22	5.00	.39
Mean	12.94	5.74	31.30	5.52	.41

* Per cell, 5 observations on each of 12 animals.

Measurement period. Tables 2*a* and 2*b* present, respectively, the amounts of food and water taken during the 1-hr. measurement periods, together with their standard deviations, and the *f*/fw, and *w*/f*w* ratios. Matched *t* tests have been made of the difference between each mean and every other mean of each table.

In Table 2*a* all differences are significant at better than the .01 level, except three: (*a*) FW*f* and FW*f*w differ between the .02 and .05 levels of significance; this *f*/*f*w ratio, however, is in conformity with ratios obtained over the 22 hr. of the ingestion period. (*b*) No significant difference appears between W*f*w and 0*f*w. Whether or not water is available during food deprivation makes little difference in the amount eaten at the end of the period *provided* it is available when the food is given. (*c*) F*f*w and 0*f* do not differ significantly. Rats that have been deprived only of water eat just as much food when water is given to them as do rats first deprived of both food and water and then given food without water.

TABLE 2

Experiment I

Food and Water Consumption during Measurement Periods

(*a*) Food Consumption (gms.) during 1-hour Measurement Periods as a Function of Preceding Deprivation Period*

AVAILABLE DURING FIRST 21 HR. OF PRECEDING 21½ HR. (DEPRIVATION PERIOD)	FOOD CONSUMED (GMS.) WHEN ONLY FOOD AVAILABLE (*f*)		FOOD CONSUMED (GMS.) WHEN FOOD AND WATER BOTH AVAILABLE (*f*w)		RATIO (*f*/*f*w)
	Mean	*SD*	Mean	*SD*	
Nothing (0)	6.03	0.89	8.97	0.96	.67
Water (W)	7.02	1.05	8.68	1.02	.81
Food and water (FW)	2.52	1.05	3.60	1.22	.70
Food (F)	1.11	0.50	5.55	0.88	.20 (*F*/*F*W = .57)

(*b*) Water Consumption (gms.) during 1-hour Measurement Periods as a Function of Preceding Deprivation Period*

AVAILABLE DURING FIRST 21 HR. OF PRECEDING 21½ HR. (DEPRIVATION PERIOD)	WATER CONSUMED (GMS.) WHEN ONLY WATER AVAILABLE (*w*)		WATER CONSUMED (GMS.) WHEN FOOD AND WATER BOTH AVAILABLE (f*w*)		RATIO (*w*/f*w*)
	Mean	*SD*	Mean	*SD*	
Nothing (0)	4.18	2.33	10.05	0.80	.42
Food (F)	14.00	3.45	15.85	3.14	.88
Food and water (FW)	3.20	1.37	4.77	1.35	.67
Water (W)	1.08	0.98	7.26	1.41	.15 (*W*/F*W* = .41)

* Per cell, 5 observations on each of 12 animals; *SD*'s with respect to 12 submeans.

In Table *2b* all differences are significant at better than the .01 level except as follows: (*a*) Between F*w* and Ff*w*; water-deprived rats drink large quantities of water irrespective of the presence of food when water is given them. The *w*/f*w* ratio deviates from 1.00 in the direction expected from the deprivation period. (*b*) Between 0*w* and FWf*w*, and 0*w* and FW*w*. The rat first deprived of both food and water, and then given water, drinks no more than an effectively satiated animal. A strong "hunger drive" seems to suppress drinking and might be said to "inhibit thirst."

The "self-imposed" deprivation reveals itself in the *w*/f*w* and *f*/*f*w ratios. The ratio reaches its maximum when, for 22 ½ hr., the animals have been deprived of the substance measured, and its minimum when the animals have been deprived of the other substance.

Food and water intakes are thus a function not solely of food and water deprivation, respectively, but of both these and of the substances available at the time of measurement. Speaking loosely, thirsty rats are hungry rats and vice versa, and the simple failure of *S* to take either food or water offered alone after the animal has been satiated with it, will predict not at all what *S* will do if presented with food and water together.

During the deprivation period, a food-deprived animal cuts down its water intake and effectively becomes water-deprived as well. Similarly, a water-deprived animal cuts down its food intake and becomes food-deprived. The present data show that effects of these self-imposed deprivations appear when measurements are made of food and water intake together in the hour following termination of deprivation.

We have performed two further experiments. In the first, we deprived the animals of water for 21 ½ hr., then for 1 hr. made different combinations of food and water available to various groups of animals. In the hour following this, we measured food intake. In the second study, a parallel procedure has been followed with food deprivation.

EXPERIMENT II

In the second experiment we deprived the animals of water for 21 hr., leaving food available (F); then allowed free access, either to food and water (fw′), to food only (f′), water only (w′), or nothing (0′), for 1 hr.; and in the following period of 1 hr. (f) measured the amount of food eaten in the absence of water. These procedures define a *deprivation period*, an *ingestion period*, and a *measurement period*.

Method

The second experiment was run through five days. The 12 *S*s, the apparatus, and basic method were the same as those used in the first experiment. At the time this experiment began, *S*s ranged from 201 to 204 days in age. The daily schedule was as follows: At 2200 all animals were given unlimited food but no water (f). At 1900 of the following day, 3 randomly assigned animals were given food and water (Group fw′), 3 were given food but no water (Group f′), 3 were given water but no food (Group w′), and 3 were deprived of both food and water (Group 0′). All food and water were removed at 2000, and at 2010 all animals were given a measured amount of food but no water (f). At 2110 all food was removed; the amount eaten was measured. At 2127 all animals were given access to food and water with supplementary lettuce. Water was removed at 2200, the beginning of the new experimental period.

Results

Table *3a* presents for the four groups of animals the means and standard deviations of the quantities of food eaten in the 1-hr. measurement period. Significance of differences was determined by *t* tests. Since the preceding experiment led us to expect particular differences, these *t* tests were one-tailed. The amount of food eaten by the first group (w′) is significantly different, at the .01 level, from that eaten by any of the other groups. Group fw′ differs, as well, from Group f′ at the .02 level. Other differences, although not statistically significant, fall in the appropriate direction and are of the appropriate magnitudes. No effects of age, or of the sampling procedure, are evident.

The eating behavior of these animals is in remarkable quantitative agreement with the behavior under analogous conditions summarized in Table 2. The data conform with the predictions based on the results of the preceding experiment.

EXPERIMENT III

In the third experiment,[5] we deprived the animals of food for 21 hr. (W); then allowed them free access, either to food and water (fw′), to food only (f′), to water only (w′), or to nothing (0′) for 1 hr.; and in the following period of 1 hr. measured the amount of water drunk in the absence of food. These procedures again define a *deprivation period*, an *ingestion period*, and a *measurement period*.

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[5] The data of Experiment III were collected by Mr. Ogden R. Lindsley in the course of another experiment performed with the senior author.

Method

Subjects. The *S*s were 48 male albino rats, run in three squads. The first squad contained 16 animals of the Hisaw strain, 119 days old at the beginning of the experiment. The second and third squads were both of the Wistar strain, aged 98 and 127 days, respectively, at the beginning of the measurements.

TABLE 3

(*a*) Experiment II

Food Consumption (gms.) during 1-hour Measurement Periods Following Various Combinations of 21-hour Water-Deprivation Period (F) and 1-hour Ingestion Periods

(each cell, 5 days' observation on each of 3 animals)

AVAILABLE IN 22-HR. DEPRIVATION PERIOD	AVAILABLE IN 1-HR. INGESTION PERIOD	GMS. FOOD EATEN IN 1-HR. MEASUREMENT PERIOD	
		Mean	*SD*
F	water (w′)	6.02	0.76
F	food and water (fw′)	2.95	0.64
F	food (f′)	1.11	0.33
F	nothing (0′)	1.61	0.97

(*b*) Experiment III

Water Consumption (gms.) during 1-hour Measurement Periods Following Various Combinations of 21-hour Food-Deprivation Period (W) and 1-hour Ingestion Periods

(each cell, 48 animals)

AVAILABLE IN 21-HR. DEPRIVATION PERIOD	AVAILABLE IN 1-HR. INGESTION PERIOD	GMS. WATER DRUNK IN 1-HR. MEASUREMENT PERIOD (1st 5 days)		GMS. WATER DRUNK IN 1-HR. MEASUREMENT PERIOD (25 days)	
		Mean	*SD*	Mean	*SD*
W	water (w′)	1.2	0.7	1.4	1.5
W	food and water (fw′)	3.2	1.0	3.8	2.0
W	food (f′)	10.5	1.9	10.6	2.6
W	nothing (0′)	1.3	0.8	1.4	1.4

Experimental room and apparatus. Throughout the experiment the rats were housed in a small internal room with one door and no windows. Two fluorescent ceiling fixtures came on at 0530 daily and turned off at 1730. A coil-type heater fan, blowing over an open vessel of water, was turned on by a thermostat. Temperatures measured at the beginning of the daily experimental sessions averaged 71.7° F, ± 3.0°, and the relative humidity averaged 67.6 per cent, ± 5.0 per cent. The cages, food, water graduates, and tubes were the same as those used in Experiment I.

Measurements. Drinking was measured with the same apparatus and methods as in Experiment I. In this experiment, however, reading accuracy was to the nearest 1 cc.

Preliminary handling. For 8 days the animals were housed in the room and stabilized on the temperature and light-dark cycle with free access to food and water. For the next 15 days the rats had free access to water, but access to food for only 1 hr. per day.

Daily schedules. The experiment proper ran for 25 days. Each day included the following operations: At 0530 the lights went on. At 1300 temperature and humidity were measured and the rats weighed. Water was next removed from pairs of cages at 6-min. intervals, and the experimental diet of the 1-hr. ingestion period was correspondingly given to the animals, according to their group memberships. General procedures otherwise conformed with those followed in the preceding experiment. The staggering was necessary because these measurements were made in the course of another experiment.

Summarizing, each animal was submitted to a *deprivation period*, 20 hr. and 50 min. in length, with access to water but no food (W). During the next hour, the *ingestion period*, the experimental groups received differential treatment. Following this, after a short delay, came a 1-hr. *measurement period*, when water alone was available. At the end of this time, each animal was given access to food for 1 hr., in addition to the water, and the experimental day was over.

Groups. Four of the 16 animals of each squad were randomly assigned to one or another of four groups, which differed in the diet given during the ingestion period. Group fw′ received food and water, Group f′ food without water, Group w′ only water, and Group 0′ received nothing.

The experiment was run through the period November, 1951 to April, 1952.

Results

No significant differences appeared in the drinking of rats of the Hisaw and of the Wistar strains. The data of all the animals under each treatment were therefore lumped and treated together.

Table 4 presents the data obtained during the first 5 days and through the whole 25 days of the experiment. One-tailed *t* tests of significance were made. Over the first five days, Group f′ differed significantly, at better than the .001 level, from Group fw′. Group fw′ differed at the .06 level from Group 0′. Over the full 25 days, all three groups differed from one another at better than the .001 level. Through neither period did Groups 0′ and w′ differ significantly from one another.

The results are in substantial quantitative agreement with those reported in Table 2. Group f′ is effectively rendered thirsty (as evidenced by drinking behavior) by the termination of the 22-hr. period of food deprivation.

DISCUSSION

The results of all three experiments are in good agreement. Food and water intake of the white rat are interdependent to a high degree. Experimental deprivation of one is associated with a large drop in the intake of the other that may be considered a "self-imposed" deprivation. At the termination of an experimental deprivation period, the rat's tendencies to eat are almost independent of whether it was deprived of food or of water.

These results confirm and extend findings already available in the literature we have cited. More important, they clarify the quantitative relationships involved.

There is reason to expect that noningestive habits acquired under food and water deprivation will behave much as do eating and drinking (7, 18, 19). More pertinently, Kendler (10) has observed a depression of food-conditioned responses when the animal is deprived of water as well as of food for 22 ½ hr., and he has found, too, that food- and water-deprived animals learn a simple T maze more slowly than animals that have been deprived of food alone. Webb (22) has also presented data showing that water deprivation controls habits that have been rewarded by food.

On the other hand, Miller, Bailey, and Stevenson (12) found that animals that have been subjected to operative techniques involving the hypothalamus may show a considerable dissociation between amounts of food eaten and the strength of behavior acquired under food deprivation with reinforcement by food.

The large size of the interaction effects we have found and the lack of strict reciprocity between food and water intakes after long periods of deprivation suggest reasons for the anomalous results in experiments on "latent learning" (6). The logical controversy over the behavior of "thirsty" and "hungry" animals loses much of its force when the assumptions that have been made, implicitly or explicitly, about the behavior of "hungry" rats toward water and of "thirsty" rats toward food prove unjustified. That "low motivation" may be a condition necessary for the exhibition of certain classes of behavior may follow from our results on simple eating and drinking.

Simple formulations of "drive" and "drive summation" such as those that have been made on the basis of Hull's 1943 theoretical treatment (9) seem to require revision. Perhaps new classes of "drives"—"latent drives" or "concomitant drives"—need to be introduced. Perhaps it will be more fruitful if these endeavors are held in abeyance until further experimentation clarifies the phenomena associated with deprivation.

Several physiological mechanisms may account for these results. Perhaps a thirsty rat cannot very efficiently eat dry food such as we used. Probably more important is the role of water in the digestive and metabolic processes (3). It is not clear, however, that the physiologists are yet in a position to give us a reasonably coherent description of the processes involved.

Further experimentation will probably have two merits: it should enable us to specify the conditions of deprivation and reinforcement associated with efficient learning, and it should provide the data which seem to us indispensible for further production of theories of drive or of latent learning.

SUMMARY AND CONCLUSIONS

Three experiments were performed on the effects of food and water deprivation on the albino rat's ingestion of food and water. In the first, the *S*s were placed on various schedules that deprived them of food, or of water, or of both food and water, or of neither, for 22 hr. After a further ½ hr. of deprivation of both, they were given food, or water, or both. Through all periods the amounts of each substance ingested were measured. Two further experiments tested hypotheses derived from the results of the first. In one, animals were deprived of water for 22 hr., and then various groups were given 1 hr. of food, or water, neither food nor water, or both. In the following hour, they were again given food, and the quantity eaten in 1 hr. was measured. In the other, a parallel design deprived the animals of food for 22 hr., then each of four groups received food, water, neither, or both for 1 hr. They were then given access to water for 1 hr., and the amount drunk was measured. From the results of these experiments, the following conclusions are drawn:

1. The amount of food eaten by water-deprived rats is some 60 per cent of the amount eaten by those which are *not* water-deprived.

2. The amount of water drunk by food-deprived rats is some 40 per cent of the amount drunk by those which are *not* food-deprived.

3. If a 21-hr. period of water deprivation is terminated, the amount of food eaten rises to some 6 gm., which approaches the amount of food eaten after a like period of food deprivation.

4. If a 21-hr. period of food deprivation is terminated, the amount of water drunk rises to some 7/10 cc., which approaches the amount of water drunk after a like period of water deprivation.

5. These increases in water and food intake are of the same order of magnitude, whether the measurement is made at the time the experimental deprivation periods are being terminated by eating or drinking, or in the period following such termination.

6. Considerable questions are raised by these results for some current treatments of "drive" and for the interpretation, in terms of so-called "irrelevant drive" and "high" and "low" motivation, of the results of latent-learning experiments involving the behavior of food- and water-deprived rats.

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CHOICE-POINT BEHAVIOR AS A FUNCTION OF SECONDARY REINFORCEMENT WITH RELEVANT DRIVES SATIATED[1]

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In the development of learning theory secondary reinforcement plays an increasingly important part. It becomes imperative, therefore, to reach a thorough understanding of its conditions. A question of special interest concerns its relation to the drives present in the organism. Will a secondary reinforcer function in the absence of the relevant drive, i.e., the drive under which it acquired its power? Estes (4) showed that secondary reinforcement acquired under thirst was effective when the animals were satiated for water but hungry. Since hunger is closely related to thirst, however, its irrelevance is uncertain. MacCorquodale and Meehl (8) showed that food and water influence choices in a T maze by satiated rats, while Myers (11) gave convincing evidence of learning under similar conditions. An interpretation in terms of secondary reinforcement implies that other objects besides food or water may become incentives for learning. The aim of the present experiment was to see if a previously neutral stimulus, after being associated with drive reduction, would reinforce a response in the absence of any relevant drive. Results should be significant for theories of how motives are acquired.

METHOD

Essentially the method was as follows: We first tried to induce a differential reaction to two cages by giving deprived rats food and water in one cage but not in the other. They were then satiated and put in a T with the two cages as end boxes, to see if they would learn to go to the positive cage even when no longer deprived. It is instructive to compare this technique with the similar one used by Saltzman (12) to demonstrate maze learning by secondary reinforcement. He, too, gave some of his rats preliminary training to two boxes with distinctive cues, feeding them in one but not in the other, and then tested them in a T with the two empty boxes as incentives. His procedure differed from ours, however, in that his rats were hungry when they ran the T while ours were satiated.

Published work (3, 9) together with our own preliminary attempts indicated that the effect we sought was a weak and elusive one. A highly sensitive test was required. We therefore adopted a method employed by Grice (5), Kendler and Mencher (7), and MacCorquodale and Meehl (8) in their studies of latent learning. This consisted of using two groups of *S*s, but instead of treating one as experimental and the other as control, pitting them against each other. Both groups were exposed to the experimental factor but in such a way that it would affect their test performance in opposite directions. Specifically, *S*s were first matched by pairs according to strength of position preference in the T. One of each pair was then fed or watered in the preferred end box, the other in the nonpreferred. When later tested in the T, any consistent difference between the two groups in strength of original preference could be attributed to the interpolated training. This factor would have acted to increase the number of preferred-side choices in the first group and to decrease it in the second.

The method described below was developed in the course of a series of pilot studies. It was then used in two experiments which are here reported separately, with the differences noted.

Experiment I

The apparatus consisted of an enclosed runway 4 ft. long, a T maze, and two cages. One cage was cylindrical with metal wall and wire floor; the other was square with walls and floor of wood. Both were unpainted. Figure 1 shows the maze with cages in position. Two black partitions concealed the cages from the choice point. Transparent guillotine doors at the choice point prevented retracing. To differentiate the two paths, they were floored with strips of linoleum, the left half painted black and the right half gray. To prevent tracking, a fresh strip was laid after each trial.

Thirst was manipulated as the primary drive, but for incentive we used a cup of water and a cup of wet mash. Total deprivation was avoided because over a long period it proved debilitating. Wet mash was introduced because a water-deprived rat is likely to eat less food than normally, and we wished to make the lure as compelling as possible. Eating in the end box was not uncommon.

The procedure consisted of the following four steps:

Adaptation. Under 22-hr. thirst *S*s were allowed 10 min. to explore the runway with water and wet mash at one end. After two or three days of this they were given two individual trials a day for four days, when all ran and drank readily. Food and water were then supplied ad libitum, and small groups were put in the empty T with all doors open 30 min. a day for three days.

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[1] Aided by a grant from the Committee on Research, University of California.

Position preference tests. On the same ad libitum schedule *S*s were put in the T and given three choices a day, spaced about an hour apart, for three days. These nine trials were used to match *S*s in pairs for strength and direction of position preference. One of each pair was assigned at random to group P, the other to group N.

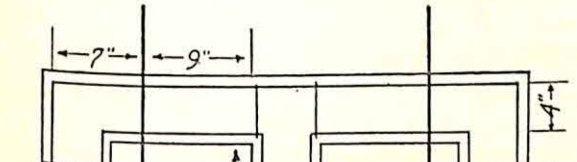

FIG. 1. Floor plan of T maze. P: partitions concealing end boxes from choice point.

Training. Differential training to the two cages was carried out under 22-hr. thirst in two parts, first in the runway, then in the T. Runway training consisted of six trials a day for six days with the metal and wooden cages alternating as end box on every trial. Each member of group P found water and mash in the cage that had been on the preferred side of the T; in the other cage were two empty cups. For group N these conditions were reversed; water and food were in the nonpreferred cage, empty cups in the preferred. Thirty seconds were allowed after entering either end box.

Trials were timed from raising the starting door until *S* entered the cage. By the end of training there was ample evidence of differential response in the presence of the two cages. On days 4 to 6, median times to the reward cage averaged 3.1 sec. compared with 6.2 sec. to the empty one.

Training in the T was designed to ensure that a strong set toward the positive cage would be conditioned to maze cues without differential strengthening of the response to be tested under satiation. For this purpose the maze was somewhat altered. No linoleum was used; the partitions were set back; elbows were removed from the paths; and, in place of elbows, end boxes were put in facing the choice point, from which they could be seen about 10 in. away. One cage contained water and food, the other empty cups, as before. Each *S* had two spaced trials a day by a correction method. If *S* made an error, it was confined for 30 sec., then given another free choice, and so on until it chose correctly. If *S* was right the first time, it was allowed 30 sec. to eat or drink, followed at once by a forced run to the opposite side. The second trial came about 90 min. later with the positions of the cages reversed. Order of position of the correct end box was reversed from day to day, R-L, L-R, R-L, and so on. Training continued in this way for nine days, when 75 per cent of the daily trials were correct and over half the *S*s were responding without error on both trials.

Satiated tests. The T was now restored to its original form, with linoleum and partitions in place and with cages concealed in their former positions. To make conditions as favorable as possible in this first experiment, the incentives were left in the positive end box and both cups removed from the negative one. Three trials about an hour apart were given every other day for a total of seven test days. Satiation was accomplished by supplying the living quarters with bottles and pellets at the close of trials the day before; 5 hr. before the next trials all food and water were removed for 4½ hr.; they were then returned along with cups of water and mash until trials were over. No eating or drinking was observed in the apparatus on satiated tests.

On a test trial the choice-point door on the side chosen was lowered to prevent retracing. Thirty seconds were permitted after entering the end box; *S* was then returned to the living cage. (The presence of other animals in the living cage could not provide differential reinforcement, nor did it involve a relevant drive.) If *S* refused to run for 180 sec., it was gently urged except at the choice point; in this case it was removed and retested later. This happened rarely.

As a precaution against extinction of any acquired preference, on alternate days *S*s were again deprived of water for 22 hr. and given runway training just as in the training trials (12).

Out of 23 mature albino males, 20 were selected by the matching procedure described in connection with the position preference tests; these completed the experiment.

Experiment II

The procedure of Experiment I was followed except for the changes noted: (*a*) The *S*s were 24 hooded rats, 12 male and 12 female, about 80 days old; they were matched for sex as well as for position preference. (*b*) The discrimination training in the altered T was limited to four days. In that time the hooded rats, probably because of better vision, reached the same level of performance the albinos had taken nine days to achieve. (*c*) Satiation tests were extended from seven to nine days. Actually 12 tests were run beyond the 9 reported here, to test the effect of interpolated extinction trials in the runway on secondary reinforcement in the T. Results are omitted for lack of space but will be referred to in the discussion. (*d*) During satiated tests in Experiment I the incentives were present in one cage. In view of the results of MacCorquodale and Meehl (8) and Myers (11) already cited, it was important to know whether our finding was due to the same factor or to the cages themselves. We therefore divided the 12 pairs of rats at random into two equal groups, one of which found water and food in both end boxes while the other found empty cups in both. The only restriction was to divide males and females equally between the two groups. It is important to note that any differential effect of the incentives was eliminated for all 12 pairs. Our reason for dividing them was to counterbalance a possible "novelty" effect.

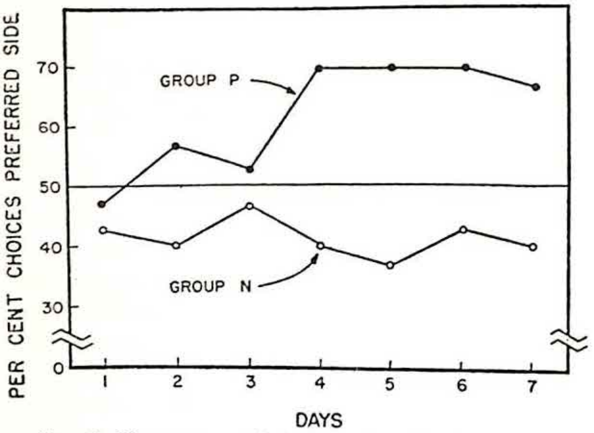

FIG. 2. Percentage of choices of originally preferred side on satiated tests (Experiment I)

TABLE I

Means and Percentages of Preferred-Side Choices Based on Total Satiated Trials

EXP.	GROUP	*N*	TRIALS	MEAN	PERCENTAGE
1	P	10	21	13.0	61.9
	N	10	21	8.7	41.4
2	P	12	27	16.2	60.2
	N	12	27	11.0	40.7

RESULTS

Experiment I

As explained above, if interpolated reward learning affected satiated performance, the effect would show up as a difference between the groups on retest of their original preference. Figure 2 shows the percentage of choices of the originally preferred side. A clear separation appears between the curves of groups P and N. Some questions are raised, however, which we cannot answer. We should expect both groups to start above 50 per cent and diverge, with group P going up and group N going down. Actually they start below the mid-line, and the divergence is almost entirely due to group P.

Over-all numerical data are included in the upper half of Table 1. Analysis of variance of the data classified by treatment, paired *S*s, and order of tests yielded one significant interaction, viz., between treatment and pairs of *S*s. Testing the variance between groups P and N against this interaction gave an *F* of 12.01, which for 1 and 9 *df* is significant at the .01 level. Interaction between treatment and order of tests, indicating *divergence* of the groups, was not significant.

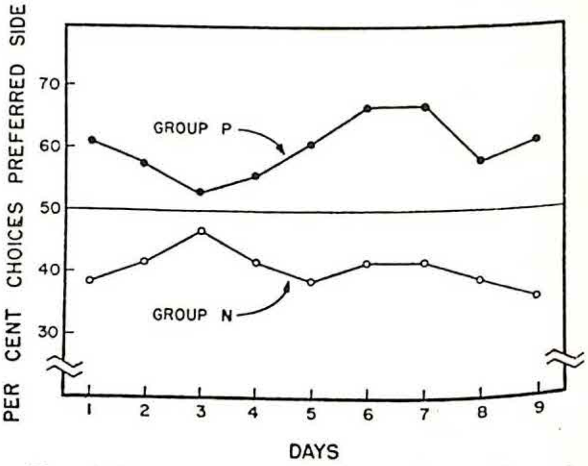

FIG. 3. Percentage of choices of originally preferred side on satiated tests (Experiment II)

Experiment II

Percentages of preferred-side choices in the nine satiation tests are plotted in Figure 3. Again the two curves are distinctly separated. This time, however, they stand apart from the beginning, and neither one shows any appreciable slope.

Table 1 summarizes the results for the 27 trials together with the corresponding data from Experiment I. The agreement between the percentages from the two experiments is quite striking. It suggests that equalizing the presence or absence of food and water in the end boxes on satiation tests made no difference in the results. Incidentally, there was no difference between the pairs that found food and water in both end boxes and those that found none in either. Analysis of variance confirmed these indications. There were no significant interactions; the relevant ones were therefore pooled to give an error estimate. For the variance between groups P and N, $F = 76.58$, significant far beyond the .001 level.

DISCUSSION

The question at issue in this experiment was whether secondary reinforcement could be demonstrated in the absence of relevant drives. Do the results justify an affirmative decision? The answer depends on what datum we accept as a measure of secondary reinforcement.

The appropriate datum in this case is indicated by the experimental design. Two groups were first equated for position preference, then so trained as to give secondary reinforcing value to opposite end boxes. It follows that the most powerful test of this effect is the difference between the groups in the measure on which they were originally matched, viz., the proportion of choices of the side originally preferred. Since this statistic is highly significant in both experiments, and since the two groups were otherwise treated alike, a positive conclusion seems justified.

It may be objected, however, that a better index of secondary reinforcement would be the amount by which the two groups drew apart on successive tests. The ground for this argument is that differential secondary reinforcement by the two end boxes should produce differential increments of reaction potential, leading to a progressive increase of "correct" choices. In short, the *S*s should learn. As already stated, by this criterion our results fall short of significance. Moreover, a breakdown of choices for the first three test trials in Experiment II shows no appreciable trend.

We are unable to dispose of this argument completely. In defense of our position the following points are to be noted: (*a*) There is a possibility of latent learning. It should be noted that before the tests all *S*s had had three 30-min. periods in the maze plus nine preference trials. That this experience should have produced latent learning measurable under these conditions is made unlikely by the negative results of Denny and Davis (2), to say nothing of our interpolated training with reversal of end box positions. On the other hand, this training took place on an altered maze; moreover, our maze paths were made more discriminable than those of Denny and Davis by the use of black and gray strips. (*b*) MacCorquodale and Meehl found the same thing in their similar study. Incidentally, their alleys were also black and gray. A clear separation between their curves appeared within the two trials of the first test day. That two studies using different methods of matching *S*s should both find such early discrimination suggests that it is not an artifact. (*c*) In an unreported extension of Experiment II, as noted above, food and water were removed from the positive end box on interpolated training trials for half the pairs of *S*s at a time. Parallel with these extinction trials the satiated test choices of groups P and N came together, abruptly in the first half tested, more gradually in the second. This finding strongly suggests the extinction of secondary reinforcement.

As the term is here used, *secondary reinforcement* does not necessarily imply the strengthening of S-R connections. In Hull's terminology it may affect ${}_{S}E_{R}$ directly rather than by way of ${}_{S}H_{R}$. Two possible "explanations" of the obtained results are suggested. The first is modeled on Spence's (14) account of the role of fractional anticipatory goal reactions in selective learning. It runs as follows: (*a*) During training a differential reaction to the positive end box (r_g) was conditioned to runway cues. (*b*) By stimulus generalization (augmented by nonspatial discrimination training in the maze) r_g was aroused at the start and choice point of the T. (*c*) In preliminary exploration and tests for position preference r_g had already been conditioned, by unspecified reinforcement, to cues on one side of the choice point, say the right; its interoceptive cue (s_g) was thus conditioned to a right turn. Similarly and to the same extent a response to the negative end box was conditioned on the other side. (*d*) On satiated test trials the s_g from step (*b*) summated with the s_g of step (*c*) to produce a greater stimulus-intensity dynamism (V), and thus a greater ${}_{S}E_{R}$, to a right turn than a left. The obtained results follow.

A second interpretation is based on the assumption that secondary reinforcement, like primary, involves drive reduction. This hypothesis implies acquired drive. Since on test trials relevant primary drives were satiated and irrelevant ones could not be reduced by the reinforcer, it follows that a new drive must have been acquired in training. The nature of such a motive cannot be specified at present. Three suggestions are available: drive externalization (1), drive fear (10), and tertiary drive (13).

A decision between these views awaits further research. That they may turn out to be closely related is foreshadowed by the following quotation from Hull: "... the understanding of the subject of secondary motivation is rather obscured by the fact that its relationship to incentive motivation ... and to the associated mechanism of anticipatory goal reactions in terms of stimulus-intensity dynamism ... has not yet been clarified" (6, p. 24).

SUMMARY

A method was developed to test the hypothesis that a secondary reinforcer would strengthen a response in the absence of relevant drives. The method consisted of three main steps: (*a*) Rats were tested for position preference in a T with distinctive end boxes and divided into two groups matched on that basis. (*b*) Thirsty, they were trained to find reward in one end box but not in the other. This training was given partly in a runway, partly in the T with positions reversed from trial to trial. One group (P) was rewarded in the preferred box, the other in the nonpreferred. (*c*) They were given a series of satiated tests in the T alternating with further runway training.

Results in two experiments were as follows:

1. In terms of choices of the originally preferred side on satiated tests, a highly significant difference appeared in favor of group P.
2. This difference occurred whether or not the presence of incentives in the end boxes was equalized on test trials.
3. There was no reliable evidence that the difference increased on successive tests.

Possible interpretations of these findings were discussed.

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SUBCORTICAL MECHANISMS IN EMOTIONAL BEHAVIOR: AFFECTIVE CHANGES FOLLOWING SEPTAL FOREBRAIN LESIONS IN THE ALBINO RAT

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During the past two decades numerous investigators have been concerned with the role of subcortical mechanisms in emotional behavior. Durable changes in affective behavior have been described for animal preparations with transection of the brain stem at the intercollicular level (Sherringtonian decerebration), neocortical ablation, lesions of the hypothalamus, lesions of the amygdaloid complex, and lesions in various parts of the thalamus (4, 11). Surprisingly little attention has been paid, however, to the behavioral effects of lesions in the septum.

The septal region of the forebrain presents a complicated anatomical picture. As shown by Figure 1, its caudal border is formed by the massive fornix column, which contains a large proportion of the fibers originating in the hippocampus, and continues behind the anterior commissure to the mammillary body. Other fibers of hippocampal origin cut through the substance of the septum, subsequently curve down in front of the anterior commissure to distribute, among others, to more anterior parts of the hypothalamus ("precommissural fornix"). In addition to such fibers of passage, the septal region contains numerous nerve cells, grouped into several nuclei. Most of the septal cell groups receive massive efferent connections from the hippocampus, while other fibers appear to reach the septal region from the hypothalamus. The region has extensive efferent connections with the thalamus and hypothalamus. A large number of such fibers leave the region with the fornix column and distribute, among others, to the anterior nuclei of the thalamus and to the habenula. Another contingent of septal efferents joins the precommissural fornix and ends largely in the preoptic area and in the hypothalamus.

By virtue of its paramedian position, the septal region can be destroyed experimentally with only minor involvement of other brain structures. Such experimental lesions must result in interference with most of the hippocampal discharge, and hence with an important contingent of paleocortical activity. Results of lesions in the septal region have been reported by Spiegel, Miller, and Oppenheimer (6) for the cat, and by Krieg (3) for the rat. In both animal species, behavioral changes in the direction of an increased tendency to rage reactions were observed. The present report describes a series of experiments aimed at a more systematic analysis of the behavioral changes exhibited by albino rats with surgical lesions in the septal forebrain region. Specifically, the effects of septal lesions upon the acquisition and retention of a conditioned emotional response, upon the magnitude of the startle response, and upon general emotional reactivity in albino rats have been investigated.

METHOD

General Procedure

Thirty male albino rats, approximately 100 days of age at the start of the experiments, served as *S*s. The animals were divided into an unoperated control group (6 *S*s) and two operated groups, one with lesions in the septal forebrain region ("septal animals," 18 *S*s) and one with lesions in the cingulate cortex ("cingulate animals," 6 *S*s). In 27 animals, a conditioned emotional response of the "fear" or "anxiety" type was established prior to operation, and retention tests were conducted postoperatively. The remaining 3 animals were operated prior to conditioning in order to evaluate the effects of the lesions upon acquisition of the emotional response. In addition, ratings of emotional reactivity and measurements of startle response magnitude were made in all 30 animals both pre- and postoperatively. Upon completion of the experiments, the animals were sacrificed, their brains fixed, sectioned, and stained in order to verify histologically the location of the lesions.

Emotional Conditioning

The conditioned emotional response was established in all animals according to a procedure previously described by Brady and Hunt (8). All conditioning trials

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[1] The authors wish to thank Mr. Irving Geller and Mr. William C. Stebbins for their help in part of this experiment.

took place in the "grill box," a cubical chamber with a grill floor, one transparent wall to permit observation, and an earphone attached to one wall for transmission of a clicking noise. All animals received a series of six conditioning trials distributed throughout a ten-day period so that no more than one trial was given on any one day. Each trial consisted of a 3-min. presentation of a clicking noise, the conditioned stimulus, terminated contiguously by two momentary painful electric shocks to the feet, the unconditioned stimulus, delivered through the grill floor of the apparatus. In this situation, the emotional response develops after a few trials as complete immobility and crouching ("freezing"), usually accompanied by defecation, upon presentation of the conditioned clicker stimulus.

Rating Scale

In an attempt to evaluate gross changes in emotional reactivity associated with septal injury, a rating-scale technique was employed. Ratings were made of all animals for the following seven behavior components: (*a*) resistance to capture in the home cage, (*b*) resistance to handling, (*c*) muscular tension reaction to capture and handling, (*d*) squealing and vocalization reaction to capture and handling, (*e*) urination and/or defecation reaction to capture and handling, (*f*) aggressive reaction to presentation of forceps in close proximity to the snout, (*g*) aggressive reaction to prodding with forceps. Previous investigations by Stone (8) and Tryon *et al.* (9) have demonstrated the efficacy of similar rating-scale techniques in the study of emotional behavior in the rat, and development of the present scale followed a procedure outlined by Tryon *et al.* (9).

A four-point rating scale was used for each of the seven behavior components. The zero point was fixed by the behavior of tame albino rats such as those conventionally employed in laboratory experiments. The ratings were performed by three independent judges in the relatively standard situation of removing the animal from its home cage and placing it in the emotional conditioning apparatus. Measures of correlation between the judgments of the three raters yielded coefficients of better than .90 for this scale. Ratings of all animals were made on three occasions preoperatively (30, 15, and 1 day before operation) and for 12 consecutive days postoperatively, starting on the first postoperative day.

Startle Response Measurement

An additional aspect of behavior selected for measurement in the present study was the startle reaction of rats to an explosive auditory stimulus. The method involved the use of a stabilimeter-like apparatus, previously described by Brown, Kalish, and Farber (9), capable of recording the magnitude of a rat's jump to a loud sound. The rat was confined in a small box (2.37 in. wide, 7.37 in. long, 5.5 in. high) surmounted upon the platform of a 5-lb. postage scale. Vertical movements of the platform were transmitted by means of a thread to an ink-writing muscle lever whose deflections were recorded on a 5-in. tape moving at a rate of .53 in. per second. The startle stimulus was produced by a 22-cal. blank pistol fired about 2 ft. from the confinement box. The exact time at which the startle stimulus occurred was registered on the tape by an electromagnetic signal marker.

Twenty-four hours prior to operation all animals were given a series of five presentations of the startle stimulus, and the heights of all jumps to these stimuli were recorded. Successive trials were administered at intervals ranging from 1 to 2 min., the average interval being about 90 sec. Again, on the day following operation, all animals received a series of five presentations of the startle stimulus according to precisely the same procedure employed preoperatively.

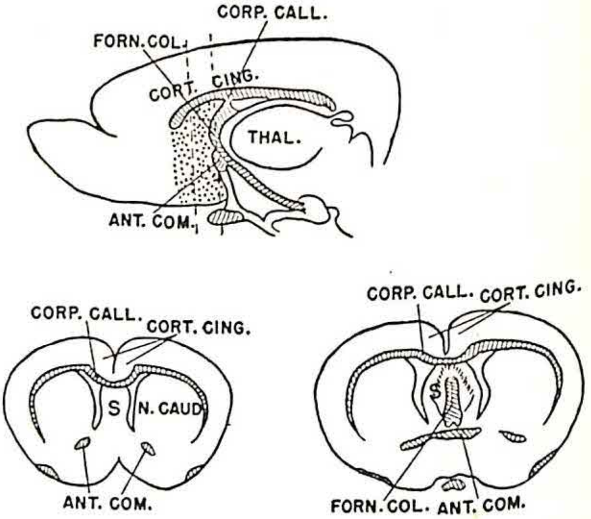

FIG. 1. Semidiagrammatic representation of the rat forebrain. Upper figure: medial aspect with septal region stippled. Lower figures: two frontal sections at levels indicated by broken lines through stippled area of upper figure. ANT. COM., anterior commissure; CORP. CALL., corpus callosum; CORT. CING., cingulate cortex; FORN. COL., fornix columns; N. CAUD., caudate nucleus; THAL., thalamus.

Operative Procedure

All operations were performed with the animals under ether anesthesia. After incision of the skin, the periosteum of the cranial vault was pushed aside, and a small burr hole was produced in the midline, 4 to 5 mm. behind the frontal pole of the cerebral hemisphere. Through this opening, a slender cutting instrument, essentially a needle with the tip bent at a right angle and sharpened sideways, was sunk between both hemispheres to a measured depth, whereupon it was rotated several times in order to ensure the production of a bilateral paramedian lesion. Upon completion of this procedure, the periosteum was stitched over the trephine hole, and the skin was closed. No bandage was applied. In most cases, the effect of the anesthesia completely disappeared within the first two postoperative hours.

Figure 1 shows a midsagittal and two frontal sections through the areas involved in the operations. On the midsagittal plane, the septum is represented by

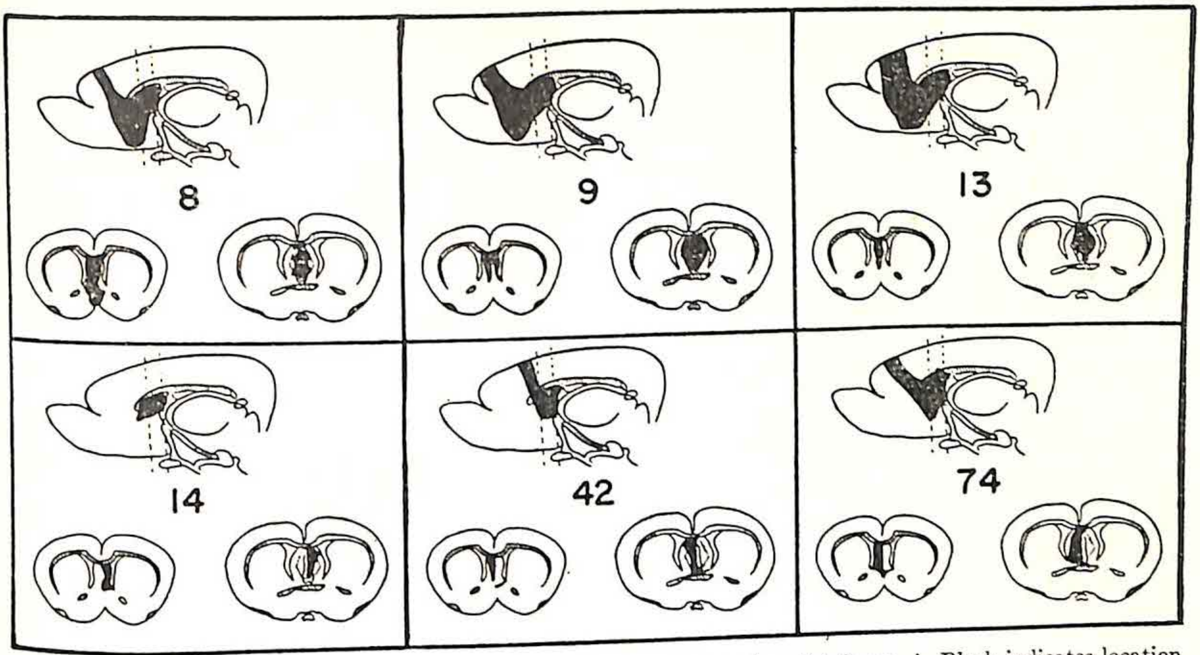

FIG. 2. Medial and frontal reconstructions of septal lesions in experimental Group A. Black indicates location and extent of the lesions in the reconstructions. See Figure 1 for orientation.

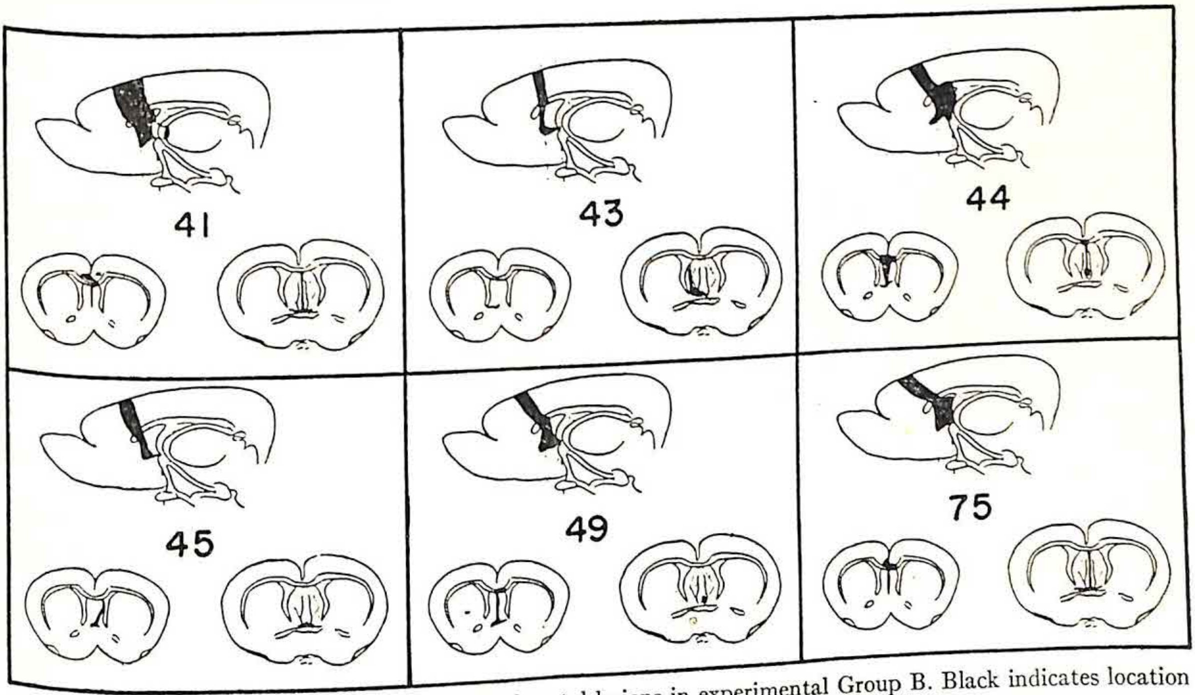

FIG. 3. Medial and frontal reconstructions of septal lesions in experimental Group B. Black indicates location and extent of the lesions in the reconstructions. See Figure 1 for orientation.

the stippled area (the anterior and basal boundaries being somewhat arbitrary), and the two broken lines through this area indicate the level of the two frontal sections depicted below. It is evident from this figure that the instrument used in the surgical procedure, on its way toward the septal region, passed between the opposing surfaces of left and right cerebral hemisphere. In many cases, this area of the cortex (cingulate cortex) sustained more or less extensive damage, while in most cases the corpus callosum was penetrated by the instrument immediately prior to its entrance into the septal region. The six operated control animals in which lesions were produced only in the cingulate cortex and corpus callosum provided a necessary control for such damage as well as for the effects which might be attributable to any operation per se.

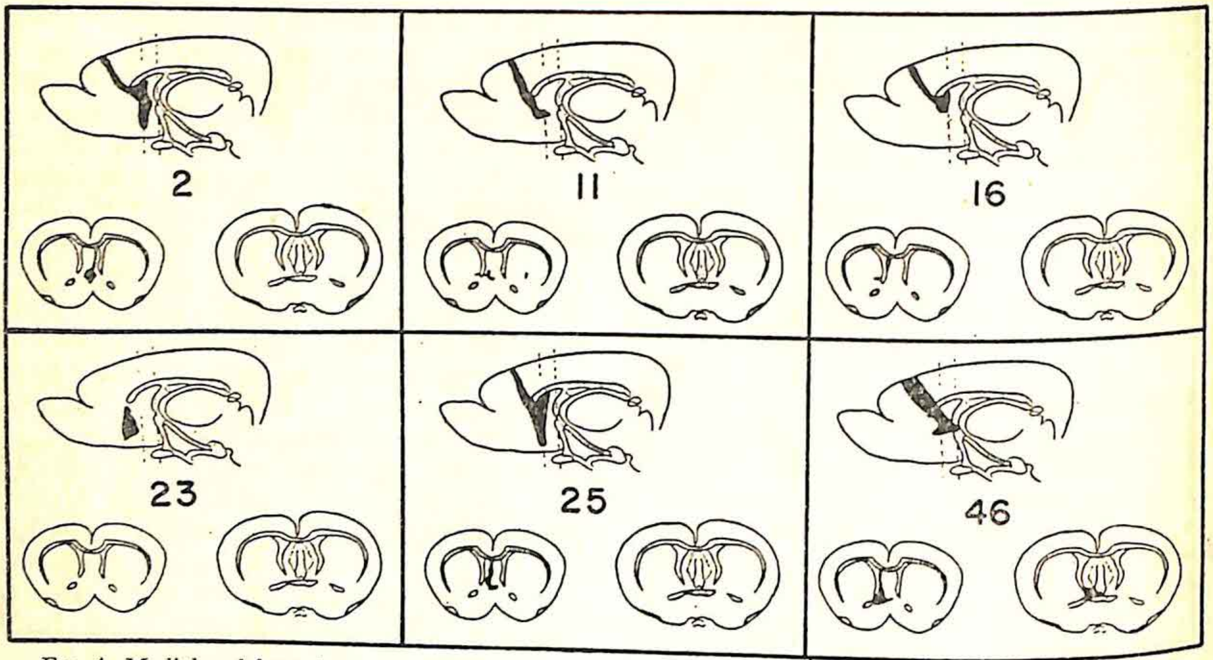

FIG. 4. Medial and frontal reconstructions of septal lesions in experimental Group C. Black indicates location and extent of the lesions in the reconstructions. See Figure 1 for orientation.

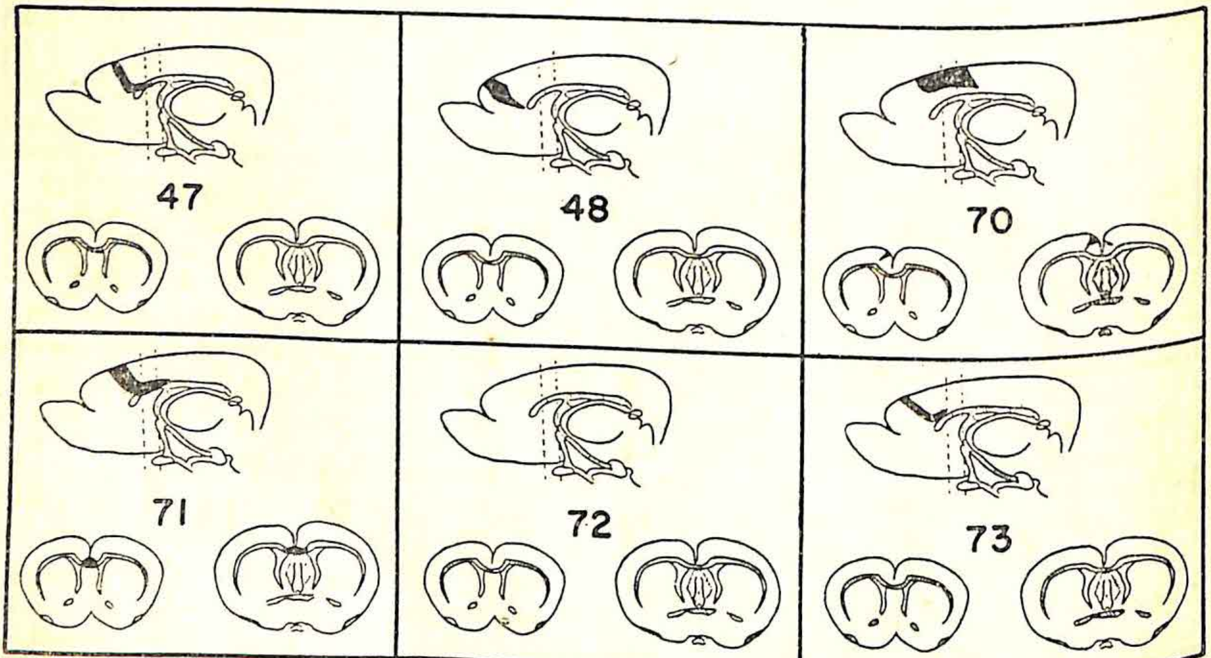

FIG. 5. Medial and frontal reconstructions of cortical lesions in operated control group. Black indicates location and extent of the lesions in the reconstructions. See Figure 1 for orientation.

Histological Procedure

Histological verification of the lesions was obtained for all 24 operated animals. The brains were fixed in 10 per cent formalin for one to four weeks following removal and were subsequently embedded in paraffin. Serial sections were cut at 20 μ, and, of each brain, two alternating series were prepared, one of which was stained for cells with thionin, and the other with a modified Weil stain for myelinated fibers. Projection drawings were then made of every fifth section of the Weil-stained series. The lesion was drawn in after observations in both the Weil and thionin series. Figures 2, 3, 4, and 5 show two of these drawings at the indicated levels together with a reconstruction of the lesion on the midsagittal plane for each of the 24 operated animals. Figure 1 is intended to serve as a key to the interpretation of these plates. Histological analysis of the brains of two of the six nonoperated control animals was also accomplished and, as would be expected, no lesions were found.

RESULTS

General Observations

Gross and dramatic changes in behavior appeared in the septal animals within 2 hr. after operation. Such animals presented a picture of striking alertness with limbs rigidly extended and eyes intently following the movements of the observer approaching the cage. The sudden presentation of almost any auditory stimulus produced an explosive startle reaction. The typical exploratory response of the normal rat to presentation of such an innocuous object as a pencil was replaced by "freezing" behavior with the vibrissae turned stiffly forward. Rapidly approaching objects were attacked immediately with vigorous biting, while a magnet-like reaction was exhibited when the object was moved slowly before the snout. Attempts to capture or handle the animal were responded to by fierce attacks on *E* alternating with vigorous flight reactions. In certain instances, merely opening the cage would provoke the animal sufficiently to have it leap from the cage and hop about the room in an odd, rabbit-like fashion. When placed in a group cage, five or six such septal animals would fight continuously and vigorously for extended periods of time with loud and frequent vocalizations accompanying much of the above behavior. None of these phenomena was observed in either the operated or nonoperated control animals at any time during the course of the experiments. A motion-picture record was prepared in conjunction with these experiments to illustrate the character of these changes following septal lesions in the rat.[2]

Changes in the Conditioned Emotional Response

By the sixth conditioning trial all animals had acquired the conditioned emotional response. All 30 animals crouched and remained immobile throughout the 3-min. presentation of the clicker, and 28 of the 30 animals defecated in response to the conditioned stimulus. No significant differences in rate of acquisition appeared, however, between the group of 3 animals (rats 2, 14, 25) operated prior to conditioning and the remaining 27 animals.

On the day following the sixth conditioning trial, septal lesions were produced in 15 more animals (rats 8, 9, 13, 42, 74, 11, 16, 23, 46, 41, 43, 44, 45, 49, 75), lesions of the cingulate cortex were produced in another 6 animals (rats 47, 48, 70, 71, 72, 73), and the remaining 6 animals served as nonoperated controls. Histological reconstruction of the lesions in the two operated groups is shown in Figures 2, 3, 4, and 5. Three days after operation, tests for retention of the conditioned emotional response were conducted with all animals by a 3-min. presentation of the clicker alone. Complete retention of the conditioned emotional response was evident in the 6 operated control animals with cortical lesions only and in the 6 nonoperated animals, as well as in the 3 animals operated prior to conditioning. All 15 animals crouched, defecated, and remained completely immobile during the clicker. In contrast, however, the conditioned emotional response appeared significantly diminished in the group of 15 animals in which septal lesions had been produced following conditioning. All 15 animals showed some movement during the 3-min. clicker presentation, and only 3 of the 15 animals defecated in response to the conditioned stimulus. This difference in frequency of defecation between the experimental septal group, on the one hand, and the operated and nonoperated control groups, on the other, is highly significant ($\chi^2 = 17.2$, $p < .01$). The septal lesions appear to have appreciably diminished the strength of the conditioned emotional response on this immediate postoperative test.

Changes in Emotional Reactivity

The results of the pre- and postoperative ratings for emotional reactivity in the 18 experimental, 6 operated control, and 6 nonoperated control animals are shown in Figure 6. It is apparent that no significant preoperative differences exist between the three groups although the operated control animals show a slightly but consistently higher degree of emotional reactivity than the other two groups. Postoperatively, however, there appears a rather marked change in the emotional reactivity of the experimental septal animals as compared to both their own preoperative level and the level of the two control groups. The difference between each of the three preoperative ratings and each of the first three postoperative ratings for the experimental septal group is significant beyond the .01 level of confidence. Furthermore, the difference between the experimental septal group and the two control groups on each of the first six postoperative ratings is also significant beyond the .01 level of confidence. The figure also shows that there is a gradual decline in the magnitude of the ratings for the experimental septal group over the 12-day postoperative rating period, so that by the ninth or tenth day, the curve for this group closely approximates that of the operated controls.

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[2] A review of this film is presently in press in the *Psychological Abstracts.*

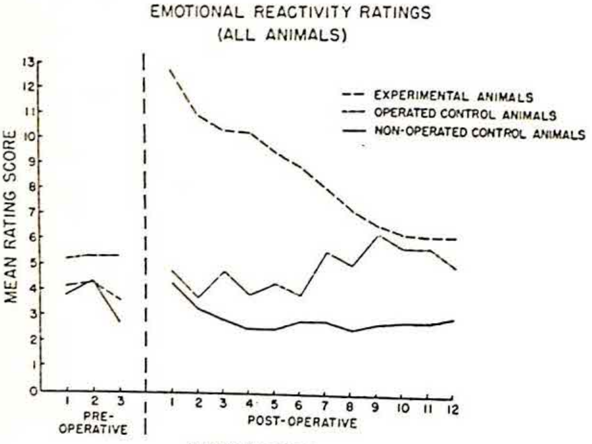

FIG. 6. Changes in emotional reactivity following experimental septal lesions

Changes in Startle Response

Table 1 shows the results obtained from measurements of the startle response magnitude both pre- and postoperatively in the experimental, operated control, and nonoperated animals. The animals' scores for both the pre- and postoperative tests represent the means of the startle responses elicited on the five trials conducted on each of the two days. Inspection of the tabulated group mean values indicates that there was no significant difference between the three groups on the preoperative test. Postoperatively, however, the experimental septal animals show a marked increase in the magnitude of the startle response, while neither the operated nor the nonoperated control animals show any such gross change in the amplitude of the response. The difference between the pre- and postoperative mean values for the experimental septal group is highly significant ($t = 3.82$, $p < .01$), as is the difference between the postoperative mean value for the experimental septal group, on the one hand, and the postoperative mean value for operated control group ($t = 3.29$, $p < .01$) and nonoperated control group ($t = 3.76$, $p < .01$), on the other. As may well have been predicted on the basis of the rating scale changes, septal lesions appear to have significantly increased the magnitude of the startle response in the experimental animals.

TABLE 1

Magnitudes of Startle Responses for Experimenta
Operated Control, and Nonoperated Control Groups
on Pre- and Postoperative Tests

GROUP	PREOPERATIVE RESPONSE IN MILLIMETERS		POSTOPERATIVE RESPONSE IN MILLIMETERS	
	Mean	*SD*	Mean	*SD*
Experimental	9.80	7.69	22.58	6.52
Operated control	10.63	8.08	9.98	7.84
Nonoperated control	8.25	5.98	9.32	6.87

DISCUSSION

The results of these experiments reflect quite clearly the critical role of certain forebrain mechanisms in the mediation of some forms of emotional behavior. The striking changes in emotional reactivity which appear immediately following lesions of the septal region in the experimental animals do not occur in either the animals with lesions of the cingulate cortex or in the nonoperated animals. The duration of these changes, however, appears to be limited. Although the present data do not permit any precise definition of this time parameter, it can be seen from Figure 6, that considerable diminution in rated emotional reactivity occurs during the first 12 postoperative days. Whether this change can be accounted for on the basis of physiological recovery with time alone, continued daily handling, or both, is presently under investigation.

Within the experimental group, however, differences did appear in both the degree and duration of the changes in emotional reactivity following septal lesions. In an attempt to provide some systematic explanation of this behavioral variation, the 18 septal animals were divided into the three anatomical subgroups of 6 animals each, represented in

Figures 2, 3, and 4. Figure 2 shows that in the animals of Group A, large lesions were found in the supracommissural part of the septal area, involving, among other structures, all or most of the components of the fornix column. Figure 3 shows that in the animals of Group B, the supracommissural part of the septal area was involved to a lesser degree, and considerable parts of the fornix column escaped injury. Figure 4 shows that in the animals of Group C, only minimal damage to parts of the septal area other than those involving the supracommissural septum and the fornix column was sustained.

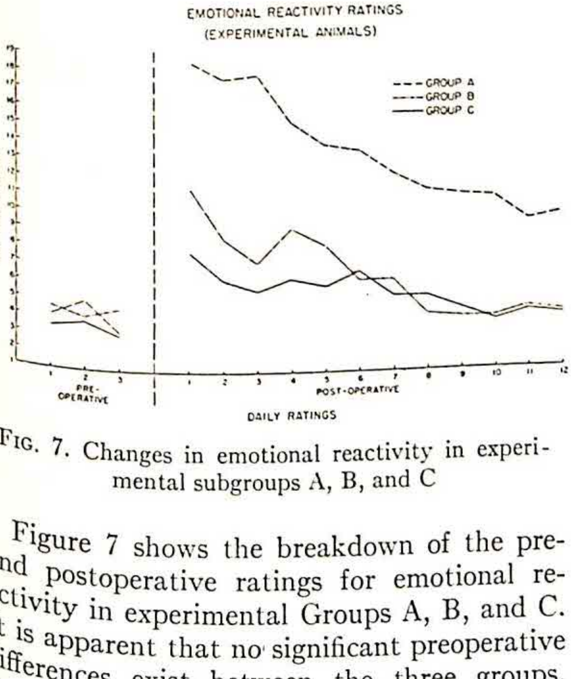

FIG. 7. Changes in emotional reactivity in experimental subgroups A, B, and C

Figure 7 shows the breakdown of the pre- and postoperative ratings for emotional reactivity in experimental Groups A, B, and C. It is apparent that no significant preoperative differences exist between the three groups. Postoperatively, however, the difference between Group A, on the one hand, and Group B and C on the other, is highly significant (.01 level of confidence for the first two postoperative daily ratings). In addition, the difference between Groups B and C on the first four daily postoperative ratings is significant well beyond the .05 level of confidence.

The fact that the intensity of the postoperative effects appears to be roughly commensurate with the extent of injury to the fornix column naturally raises some doubt as to the "septal" nature of the behavioral phenomena observed in this study. The classical concept of the fornix column as consisting of fibers originating in the hippocampus would indeed tend to justify an interpretation of the findings described above as the result of interference with a hippocampal mechanism. As pointed out above, however, the fornix column, at the level where it was severed in the present experiments, receives a large number of nerve fibers arising from the septal gray matter and distributing, among others, to the anterior nuclei of the thalamus (10), to the habenula (7), and to the hypothalamus. The present experiments leave it an open question whether the behavioral effects of septal lesions are due to interruption of such septodiencephalic connections, or to interference with the massive hippocampo-hypothalamic discharge pathway contained in the fornix column, or to both. A possible role of direct hippocampal projections to the brain stem in affective behavior could obviously be demonstrated only by bilateral interruption of the fornix system proximal to the level where it receives its contribution from the septal nuclei. Such experiments, however, will be complicated by substantial and hardly avoidable injury to adjacent brain structures.

The effect of the experimental septal lesions in decreasing the strength of the conditioned emotional response, however, presents an apparent paradox when the marked increase in general emotional reactivity found in the same experimental animals is considered as an effect of such lesions upon the emotional repertoire of the organism considered as a unitary instinctual pattern. At least two possible explanations for this apparent inconsistency present themselves. First, the change in the conditioned emotional response may represent only a nonspecific effect of septal ablation upon previously learned behavior in general, so that the decrease in the strength of the previously conditioned "fear" response may not necessarily be related to the emotional character of the reaction per se. That is, septal lesions might increase general emotional reactivity on the one hand while impairing the retention of any previously learned behavior on the other.

Secondly, the apparent inconsistency between the two "emotional" changes in behavior following septal ablation may be related to a confounding of the two effects in the postoperative test for retention of the conditioned emotional response. That is, postoperative presentation of the conditioned clicker stimulus to the experimental septal animals may have elicited an unconditioned movement reaction specific to their hypersensitive physiological state which tended to occlude somewhat the previously conditioned "freezing" response. Experiments are presently in progress to test these two possibilities, as well as to evaluate the duration of the changes in emotional behavior following septal lesions.

SUMMARY AND CONCLUSIONS

The present report describes a series of experiments investigating the behavioral changes exhibited by albino rats with surgical lesions in the septal forebrain region.

Thirty male albino rats were divided into an unoperated control group (6 animals), and two operated groups, an "experimental septal" group (18 animals) and an operated control group with lesions of the cingulate cortex (6 animals). Both pre- and postoperatively, data were collected on all animals with respect to (*a*) the acquisition and retention of a conditioned emotional response (CER) of the "fear" or "anxiety" type, (*b*) the magnitude of the startle response, and (*c*) general emotional reactivity as reflected in a seven-item rating scale.

Upon completion of the behavioral observations, the animals were sacrificed and the lesions reconstructed histologically.

1. Significant increases in both emotional reactivity and startle response magnitude were found in the "experimental septal" animals postoperatively. No significant change could be observed in either the operated or nonoperated control animals. In addition, the septal lesions were found to have appreciably diminished the strength of the previously conditioned "fear" response although such lesions appeared to have no effect upon the acquisition of this response.

2. The magnitude of the changes in the behavior of the experimental septal animals appeared to be roughly commensurate with the extent of injury to the fornix column, suggesting the possible importance of this complex paleocortical fiber bundle in the transmission of neural impulses involved in determining affective behavior.

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BIOELECTRICAL POTENTIALS AND MENTAL EFFORT: I. CARDIAC EFFECTS

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Two principal cardiac effects will be described in the following pages: (*a*) the effect of mental effort on cardiac frequency and (*b*) the effect of mental effort on the integrated cardiac bioelectrical potential. The two phenomena are related to each other and give further light on the cost of "mental work."

We have no intent to settle the dispute over the definitions of the words "cost," "work," and "fatigue." Costs are dependent on the medium of exchange, which is valued differently by various writers: oxygen consumption of the body in total is one way of looking at the problem; wear and tear on local body parts is another; life span involves still another viewpoint. We shall never settle the definition of physiological costs until we have more local facts.

Facts concerning the relation of cardiac frequency (pulse speed) to psychological processes are so well known that very little more may be expected for this topic alone. A few of the early references to it are Ladd and Woodworth (11), Billings and Shepard (3), Blatz (4), Skaggs (13, 14), Darrow (6), Boas and Goldschmidt (5), Baker (1), Shock and Schlatter (12), and Benedict (2). Several have noted that sudden attention given to almost any stimulus is followed by a highly reliable and consistent increase in cardiac frequency. Benedict has noted that this is one of the most sensitive of all the circulatory indices that accompany mental effort. It is true that some interpret this cardiac effect to be the result of an emotional condition characteristic of the shock of a mental change and, therefore, most likely to be found at the immediate onset of a shift in mental set. We shall show that this is not necessarily true for all *S*s or all situations. Cardiac frequency rise can sometimes be a sustained phenomenon over a period of time, if the mental effort is continuous.

No such volume of work has been done on the quantification of the cardiac potentials, however, and in fact not until very recently have there been equipment and trained workers. The integrated bioelectrical output of a given local region constitutes one of the few ways it is possible to arrive at an index or estimate of "local costs." It is entirely possible that *local costs* may have a more significant relation to welfare and the life span than any measure in terms of such general costs as working metabolism in relation to basal metabolism. The latter dilutes local effects with unwanted measures. It is perfectly possible that the work output of a local part may rise 500 per cent while the O_2 consumption of the body in total rises less than 2 per cent, just as the efficiency of a large machine may be threatened by the stress placed on one small wheel.

METHOD

Apparatus

A description of the electrical apparatus for these experiments has already been published (8). Essentially it consisted of high-gain amplifiers feeding into a graphic recorder, producing a typical cardiogram, myogram, and encephalogram from electrodes attached over heart, muscle, and brain. From these same electrodes branching channels were sent to the bioelectric integrator, an instrument which in effect draws a straight line along the "electrical average" of output curve variations, folds the lower half upon the upper half, and then adds the curve area for any predetermined time. It is thus possible to measure the relative changes in energy picked up by the electrodes for control versus experimental periods of time. Recording was fully automatic, with a microfilm camera taking pictures of the meters which indicated the answers coming from the electronic integrator.

Filters of the lines feeding the integrator were set to respond to any frequency of 500 cps down to 1 cycle in 2 sec. Electronic noise was measured by substituting a "dummy subject," which was essentially a variable resistance having the same value as the skin resistance of the human *S*, and integrating the noise. This noise level was subtracted from the *S*'s readings. It never amounted to more than 2 per cent of the total.

Procedure

The *S* lay supine on a cot, hands at his sides, with pillows under head, knees, and forearms carefully arranged to make postural tonus unnecessary. Cardiac electrodes were attached to the region over the apex and sternum. Another pair of electrodes was attached to the region over the left frontal lobe and left ear lobe.

In the later experiments a third pair was attached to the area over the flexor arm muscles.

The *S* had previously agreed to do mental arithmetic problems, which began with an announced number from the intercommunication speaker. Upon receiving this number, *S* mentally multiplied the number by 7, then divided the product by 6, and dropped any remainder. Then this number was again multiplied by 7, the product divided by 6, and the remainder dropped, and the procedure continued in this fashion until *S* had worked as many steps as possible. Some *S*s wanted to use progressions, decimal fractions, and other substitutes for getting solutions, but the dropping of remainders made it difficult to find a good substitute procedure, and all but one *S* finally gave up trying to find short cuts.

The timing was arranged in a series of 3-min. intervals such that mental work periods alternated with rest periods, and *S* was told that during either one, all voluntary movement was strictly forbidden. Bioelectrical output was integrated separately for both rest and work periods. Between these 3-min. periods was inserted a 36-sec. intermission for giving instructions, receiving answers, and allowing *S* to make minor adjustments for maintaining freedom from postural strain. No integrations were made during the intermission periods, since the potentials from voluntary responses would have been too violent to receive with all gain settings at resting levels.

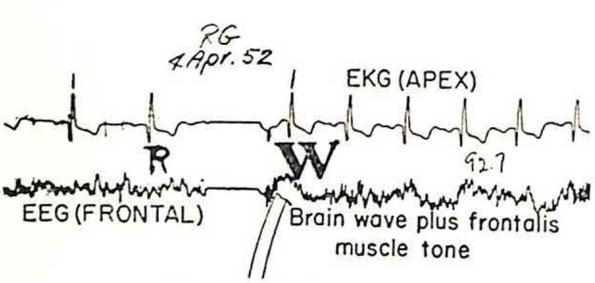


FIG. 1. A typical tracing

It is thus clear that we mean by "pure" mental effort a situation such that the integrations could be made with no speech involved, no sense organ adjustment, and the very lowest postural tone possible. Some of the past experiments have required *S*s to read a paper, recite answers, or listen to instructions. It can hardly be said that such situations provide measures of the body concomitants for mental work. In our experiments the integration was not started until *S* was about 5 sec. into the task, and it was stopped before the answer was requested.

Since the object was to determine the potential rise during work as compared with an equal rest period, it was important that *S*s really relax. Therefore, before work started all *S*s were given two or more successive rest periods to practice relaxation by a method which somewhat remotely resembled Jacobson's (9). It was here that we used facts already disclosed by Kennedy and Travis (10). The myogram from either the forehead (*m. facialis*) or the forearm is an almost perfect indicator of the degree of relaxation achieved. This is true, although we distinctly disagree with their conclusion that the myographic output could be used as an "alertness indicator." We found that a completely relaxed *S* would produce resting potentials not to exceed 4 microvolts in amplitude, and that these were totally lacking in the spike transients characteristic of any degree of muscle tension. If *S* showed instant capacity to relax, the work began immediately; if he did not relax, he was given further practice periods.

Subjects and Nature of Data

There were 20 *S*s, all male college students who were paid an hourly rate. However, one *S* consistently refused to follow instructions and finally quit before all the runs were completed. He is not included in the calculations of results, but his measurements are shown in the tables. In any such experiment as this, it must be admitted that the level of motivation is one of the determinants of individual differences in the measurements.

Figure 1 shows a typical cardiogram accompanied by a frontal encephalogram. It reads from left to right. On the left side at *R*, *S* is relaxed at the end of a rest period. In the middle, the straight line shows the intermission of 36 sec. (equipment turned off) when *S* is being given his number for the problem. At the right, beginning with *W*, is the beginning of the mental work period. Note that the spike potentials of *m. facialis* are superimposed on the brain wave. Whereas the distance between cardiac notches at *R* is such as to indicate 69 pulses per minute, at *W* the distance between notches is such as to indicate a frequency of 92.7. The data on frequencies were secured by measuring the distances of successive groups of five notches and converting the figure to frequency per minute. The measurements for a rest period were then computed for the mean and standard deviation, and the same was done for a mental work period. From these values it was possible to arrive at the critical ratios for the difference in mean frequencies of work and rest periods, respectively (Table 1).

Each "run" consisted of nine 3-min. periods, always beginning with a rest period and ending with a rest period, in alternate rest-work order, five rest periods and four work periods. If *R* designates a rest period and *W* a work period, then the first half of a run is considered to be R, W, R, W, R. But the third R will also be included in the last half as a similar R, W, R, W, R. The integrations of the two W's are averaged together to give the mental work value. The integrations of the three R's are averaged together to give the rest value. The reason for beginning and ending with a rest is that sometimes there is a drift steadily downward in the size of the integrations, and it would not be fair to compare a terminal work value with an initial rest value.

The reason for presenting the first half of a run separately from the last half of a run is the phenomenon of adaptation. As *S*s get "adjusted" to their task, they show less tension, and the physiological changes become more uniform and consistent. In other words, mental effort is heightened by the strangeness of a task, and this may involve emotional tone.

RESULTS

Table 1 shows the averages for the 20 *S*s, including the one who was uncooperative (listed as Y). The *S* designated as X is included in the computations, although he was frightened of the entire situation. He was a foreign student with superstitious ideas concerning psychologists, apparently, but cooperative. All other *S*s achieved a reasonable degree of relaxation during rest periods, and on three occasions *S*s went to sleep. They were awakened during the intermission, and work went on.

TABLE 1

Cardiac Bioelectrical Potentials and Frequencies during Mental Work

Percentages of increase for work periods as compared with rest periods, for the first halves and the second halves of the runs. The *S*s are arranged in the order of their magnitudes of increase of potentials during the first halves of the runs. *CR*, the critical ratio of the difference in means for frequencies.

	CARDIAC POTENTIAL		CARDIAC FREQUENCY			
Initials	Av. % 1st Half	Av. % 2nd Half	Av. % 1st Half	*CR* 1st Half	Av. % 2nd Half	*CR* 2nd Half
LG	+11.0	+2.7	+10.3	12.7	+5.0	6.1
RG	+9.4	+0.8	+6.4	5.1	+2.2	2.0
RPG	+7.1	+5.6	+12.9	7.4	+11.8	6.3
WHM	+6.9	+3.9	+7.2	5.9	+7.7	5.0
WLR	+6.9	+5.3	+12.1	13.7	+10.8	10.1
RHS	+6.6	+6.7	+11.9	11.1	+8.5	9.1
SCL	+6.2	+3.8	+3.3	2.1	+2.5	1.2
NS	+6.2	+1.0	+5.5	3.9	+1.2	2.2
HEK	+6.1	+5.9	+10.5	7.2	+8.5	8.5
VFS	+6.0	+5.1	+11.8	12.8	+8.0	9.1
RCB	+5.9	+4.6	+15.7	20.7	+11.3	21.4
FOA	+5.6	+4.1	+16.5	18.4	+11.5	13.8
CGS	+4.8	+6.8	+17.8	16.2	+17.7	17.1
OHA	+4.8	+6.6	+18.9	12.7	+18.7	11.1
AM	+4.3	+6.3	+11.9	12.7	+15.2	13.9
JWG	+3.8	+3.1	+4.6	4.5	+4.0	4.3
MSK	+3.5	+3.3	+0.6	3.2	−1.3	2.1
CS	+2.4	+0.8	+8.8	10.4	+6.7	7.0
X*	+0.1	−0.1	+8.6	9.1	+4.5	5.5
Y†	−12.5	+2.0	+8.9	6.6	+0.2	1.3

* An *S* with severe emotional disturbance during runs.

† An *S* who was uncooperative and consistently refused to follow instructions.

This table shows that the average expectancy is that the electrical energy put out by the heart, measured at this location, rises about 6 per cent during mental work, as compared with the rest periods, for the first half of the runs. This "local cost" drops to about 4 per cent for the second half of the runs because of gradual adaptive effects.

However, it is important to note the extremes. One *S*'s cardiac electrical output rose 11 per cent during mental work. During the first halves of runs, 6 of 19 *S*s showed no sign of adaptation, with heart potentials integrating during the second halves as high as, or even higher than, the first half. Whether this signifies sustained effort or continued frustration, we cannot be certain, but it may be significant from the viewpoint of costs.

TABLE 2

Adaptive Cardiac Effects

Comparison of Means, First and Second Halves of Runs

Mean percentage increase for mental work as compared with rest periods for 19 *S*s, first halves and second halves of runs. The critical ratios for the difference between means computed with the formula for correlated paired scores.

CARDIAC MEASURE	MEAN 1ST HALF	MEAN 2ND HALF	DIFF.	CR	*p*
Potential output	+5.68	+4.026	1.654	2.48	.03
Frequency	+10.28	+8.36	1.92	3.77	.15

However, the trend toward lower integrations during the second halves is strong enough to make the difference in means significant at the .03 level, as shown in Table 2, while a similar shift in cardiac frequencies, due to adaptation, has a confidence level of .15.

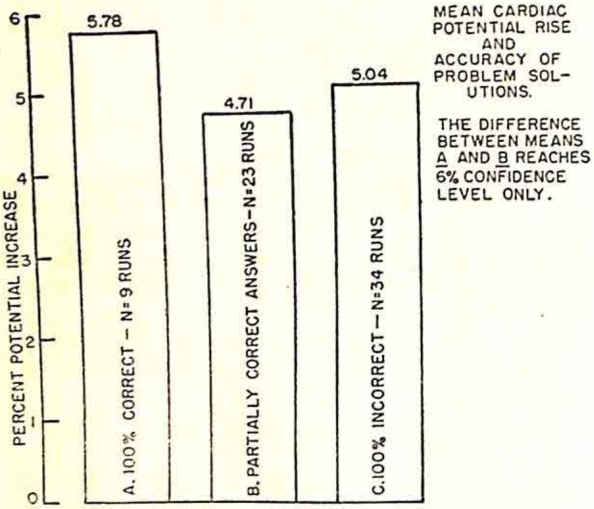
The relationship between cardiac potential output and cardiac frequency is not simple. Both show predominantly as rises during mental work. For the first halves, however, the product-moment correlation between heart potentials and pulse frequencies is only + .05. For the second halves the correlation becomes + .78 (with a probable error of .09), showing that strong agreement has appeared between potentials and cardiac frequency.

By and large, the percentage of increase for frequency is greater than the percentage of increase for potentials. This means that the trend is for the heart to beat faster, but each beat is *shallower*. If each beat remained just as strong, then potentials would be proportional to frequency, and this is not the case.

However, note that the relationship may be better presented in the form of case types:

1. During the first halves of runs, 12 of 19 *S*s showed the tendency for frequency to rise by a greater percentage than integrated potentials. This is the type in whom the heart beats *faster and shallower* during mental effort. During the second halves of the runs 16 of the 19 fell into this classification.

2. During the first halves, 3 *S*s showed percentage increases for frequency which were just about the same as the rises for integrated potentials. During the second halves, only 1 *S* belonged in this category. This is the type in whom the heart beats *faster and with equal volume*.



MEAN CARDIAC POTENTIAL RISE AND ACCURACY OF PROBLEM SOLUTIONS.

THE DIFFERENCE BETWEEN MEANS A AND B REACHES 6% CONFIDENCE LEVEL ONLY.

FIG. 2. Cardiac integration and accuracy

3. During the first halves, 4 *S*s showed the phenomenon of a percentage increase in integrated potentials greater than the increase in frequency. There were two such *S*s during the second halves. This is the type in whom the heart beats both *faster and stronger*.

It is practically certain that some readers will raise the following distinction: It isn't the thinking per se which causes the additional strain on the heart, but the emotional tone which does it. Davis (7) faced that point in his study of muscle tone. It is the fear of failing, the dislike for the task, the frustration after mistaken calculations—all emotional effects. And just as Davis made a check on the difference between correct and incorrect calculations (assuming that the latter involve frustration), so we shall also see if this has any validity.

Figure 2 charts all that we can find. The mental work was difficult. The *S*s generally knew when they were wrong, without being told. They would forget their numbers and have to start over. But we wanted a task so difficult that there would be no chance of ending with neutral findings. The 66 runs in Figure 2 represent those on which there were unquestioned checks for accuracy out of the total of 76 runs for the 19 *S*s. The 10 omitted represent cases where *S* could not remember what his last answer was when asked.

Whereas Davis apparently found that muscle tone was higher on wrong answers, this table shows that the nine runs with perfect calculations had the highest integration. However, the difference between columns A and B has a confidence level of only .06. There is certainly nothing here which is a striking proof that frustration is the cause of increased tension in the cardiac system under the conditions of this experiment.

With regard to the assumption that the cardiac changes are largely initial shock effects, certainly the frequency measurements showed no strong evidence. Those *S*s (see Table 1) who had critical ratios of 5 or higher for the difference in means between rest and work periods often showed records where the highest frequency in the rest period never reached the value of the lowest frequency in the work period. In fact, the tendency for the higher frequency to be sustained throughout the work period was the rule, with but few exceptions. Although similar observations were not possible for the potentials measurements in all *S*s, changes in circuit introduced in the later parts of the experimental series made it possible to take a series of short samples of integrated potentials throughout the work period, and this only verified the trend as shown by frequency counts. The cardiac stress tends to remain throughout a work period.

SUMMARY

1. The bioelectric output of the heart can be measured by the use of an electronic integrator and constitutes a partial work index of that organ.

2. With all needs for body movements or

postural tone removed, pure mental effort involved in arithmetical computation raised the electrical output of the heart approximately 6 per cent, and for one *S* as high as 11 per cent.

3. The majority of *S*s showed gradual adaptation and lower potential readings for the last half of each run, but there were several *S*s who either showed no improvement or even showed increased potentials as the experiment progressed.

4. The majority of *S*s, during the mental work periods, showed higher frequencies with shallower potentials for each beat. But there were *S*s who exhibited faster beats of the same electrical amplitude, and some even showed faster beats with higher amplitudes for each beat.

5. There was a very low significance for the relation of potential output to the correctness of the work done, and that was in the direction of higher potentials for the more accurate workers.

6. During a given work period the cardiac stress, measured by either frequency or potentials, tends to remain high.

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EFFECTS OF CHANGES IN ARTERIAL OXYGEN AND CARBON DIOXIDE UPON COCHLEAR MICROPHONICS[1]

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Among the considerations which first arise as we study the production of cochlear microphonics is a description of how the structures which generate them use certain materials considered fundamental to metabolism. The most important of these substances for vertebrate cells is oxygen. Effects of hypoxia and anoxia upon the microphonics have been studied in several investigations (e.g., 2, 3, 4, 9, 12). The most complete experimental approach to this problem is that of Wever, Bray, and Lawrence (11), and a good recent summary of the changes in the microphonic response of the cochlea with death is given by Riesco-MacClure, Davis, Gernandt, and Covell (6, p. 158).

Ideally, an experiment intended to relate a respired gas to a selected index of activity of an organ, tissue, or group of cells should enable us to describe the relationship at least as a function of (*a*) duration of exposure to the gas and (*b*) some measure reflecting its effective concentration. We have been particularly concerned with the latter. In view of simple and reasonably accurate methods now available for measuring concentrations of gases in small samples of blood, we are of the opinion that it is time to provide greater refinement in information than can be obtained by depending upon analyses of inspired gas mixtures.

METHOD

Twenty-two cats were anesthetized with Dial with Urethane® (Ciba). To a tracheal cannula was attached a system of very small one-way valves contained in a short piece of tubing which operated in such a way that the cat inhaled through one orifice, which could be connected with a resuscitator, and exhaled through another. There was a volume of less than 3 cc. between the valves and the cannula. Both femoral arteries were exposed to provide sources of arterial blood. Each blood sample was analyzed as soon as possible. Determinations of arterial oxygen and carbon dioxide were made in duplicate by the methods outlined by Roughton and Scholander (7, 8) with the exceptions that the traditional Van Slyke procedure was used for cats 57, 60, and 61. Hemoglobin was evaluated by means of the clinical Hellige Hemometer. Cochlear potentials were obtained between a platinum-foil electrode touching the round window and an "indifferent" electrode clipped to deep tissue exposed by the incision to the bulla, and after amplification were led to a General Radio Type 736-A wave analyzer. Except in the case of cat 31, with which a 1000-cps tone was used, the stimulus was a 4000-cps tone led to the ear through a short piece of rubber tubing inserted into the external meatus. It was hoped that with a stimulus frequency of 4000 cps and a response of the order of 100 microvolts (11, Fig. 8), the measurement of neural activity would be minimized, and distortion caused by overloading the ear would be avoided.

In a few instances (cats 31 and 33, the administration of CO_2 to cat 48, and rarely when pure O_2 was given) gases other than air were breathed spontaneously from a rubber bag kept partly filled by additions from a storage cylinder. Otherwise, except for satisfactory unaided breathing of room air, rate and depth of respiration were kept fairly constant at 12 cpm by means of a McKesson resuscitator minus the safety valves between its interior and the outside. The resuscitator could be connected with or removed from the cat in a few seconds, and was operated before it was needed for a sufficient time to fill the tube leading to the cat and thus to insure rapid administration of the intended concentrations of gases.

RESULTS

Effects of Hypoxia upon Cochlear Microphonics during Hypoxia

Oxygen content of arterial blood and fall in microphonics during hypoxia. Figure 1 shows the relationship between volumes per cent of oxygen in arterial whole blood during hypoxia, and the percentage drop to the smallest microphonic output reached while this condition prevailed. Cats which showed no reduction and those which actually maintained increases are located upon the ordinate. Cats which are thought not to have completed the "acute" decline[2] ordinarily reached within a few minutes from the beginning of hypoxia are excluded, as are animals whose curves approached the limits set by complete anoxia and death. The percentage fall in the latter would obviously be meaningless because of its dependence upon the voltages which were arbitrarily elicited in the beginning. It is clear that the decline in cochlear output increases with deprivation of oxygen. The following statements may also be made: (*a*) Small changes in the amount of oxygen carried by the blood have much greater effects upon cochlear response when hypoxia is severe (e.g., below 3 vol. per cent). (*b*) Even moderate degrees of hypoxia (below 9 vol. per cent) appear to depress microphonics to some extent. (*c*) The absolute variability of the effect of hypoxia upon the size of the cochlear response is apparently greater for lesser degrees of hypoxia. The belief that our results are dependent upon the degree of experimentally induced hypoxia rather than upon adverse conditions of our animals or acoustic overloading prior to hypoxia is supported by the absence of relationship between the members of the following pairs of variables: (*a*) the level of cochlear response prior to hypoxia and fall in microphonics during hypoxia, (*b*) duration of the decline during hypoxia (from beginning of hypoxia to lowest level of cochlear response) and initial output, (*c*) vol. per cent of O_2 before hypoxia and drop in microvolts during hypoxia, and (*d*) vol. per cent of O_2 before hypoxia and duration of fall in microphonics during hypoxia.

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[1] This is a condensation of a full report (14), which may be obtained from the authors.

[2] The minimum was arbitrarily chosen by inspection of graphed data as the point at which the curve appeared to turn definitely toward horizontal or to rebound at the bottom. It was found that such a point (or limited range) was the most easily selected of various possibilities considered. For various reasons, a

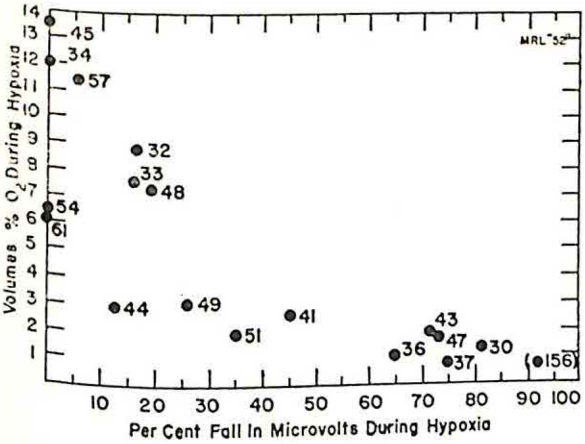

FIG. 1. Arterial oxygen and fall in microphonics during hypoxia

Recovery of cochlear microphonics during hypoxia. We shall group together, under the heading of "recovery," initial rises during hypoxia and increases following a decline, regardless of whether recovery is complete and whether it exceeds the cochlear response at the onset of hypoxia. There was no relationship during hypoxia between arterial oxygen content and the amount of increase in cochlear response *above* the initial level. This was true whether or not the rise was preceded by a decline. In fact, a transitory increase has been seen after clamping the trachea. Most cases of recovery (14 out of 16) began within the first 5 min. after onset of hypoxia, and there were some cats (e.g., 37, 41, 61, 156) which evidenced more than one clear recovery. There was no discernible connection between arterial oxygen content during hypoxia on the one hand and either the latency of recovery or the time elapsing between the beginning of recovery and its maximum on the other. Figure 2 shows that the percentage of recovery during hypoxia tends to increase as the amount of oxygen in the arterial blood increases. We have not observed a case of complete recovery during hypoxia and following a decline in microphonics when arterial oxygen was below a value between 2 and 3 vol. per cent.

Explanations of patterns of microphonic recovery during and after hypoxia, and especially of variability in response to lesser degrees of hypoxia, must consider adaptive changes elsewhere in the organism which could diminish or counteract effects of oxygen deprivation upon the structures within the cochlea (1, 13). The possible role of the spleen should by no means be underestimated in this connection (5). With the nature of these adjustments in mind, we should realize that those animals which showed a diminution in cochlear output during relatively mild hypoxia probably reveal more accurately than the others the true sensitivity of the microphonic generators to reduction in their supply of oxygen.

Recovery of Cochlear Microphonics after Hypoxia

Arterial oxygen content during hypoxia and subsequent recovery. Our data deal only with

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few animals were returned to air or oxygen before the full effects of hypoxia became evident. Data obtained from these cats have been used in other connections whenever meaningfulness has not been impaired by this fact.

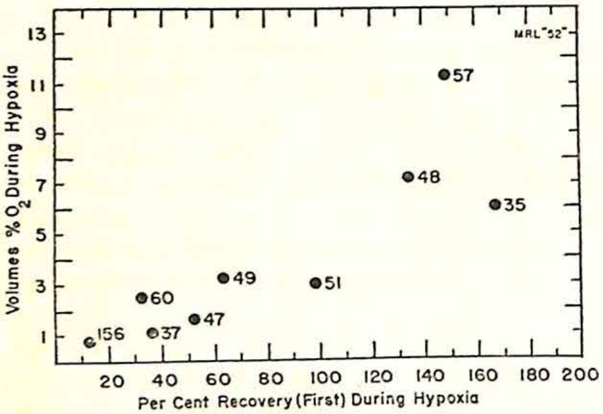

FIG. 2. Arterial oxygen and recovery of microphonics during hypoxia

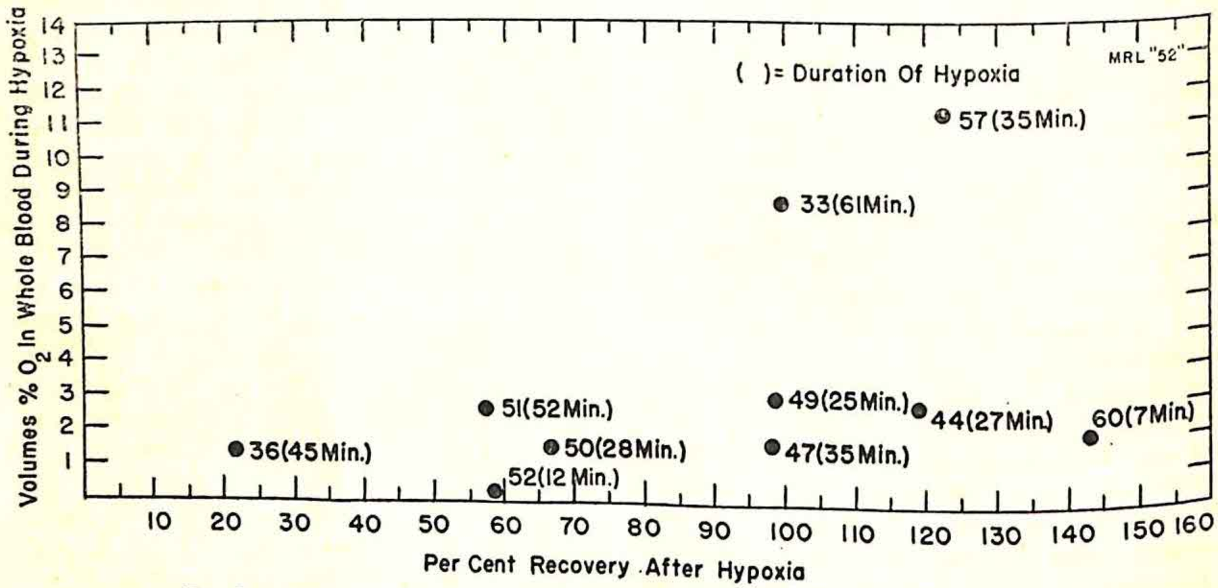

FIG. 3. Arterial oxygen during hypoxia and posthypoxic recovery of microphonics

recovery within the first several minutes to few hours following hypoxia. Figure 3 shows that complete recovery is possible after arterial blood has contained as little as 2 to 3 vol. per cent oxygen for a period long enough to allow the microphonics to reach a rough equilibrium (about ½ hr.). Conversely, no instance of full recovery was found for values significantly below 2 vol. per cent. Perhaps some of the variability which is seen may be attributable to the lack of constancy of duration of hypoxia. Figure 4 reveals an inverse relationship between arterial oxygen below 3 vol. per cent and the time required to reach maximum recovery after hypoxia. When the fall in microvolts is greater than approximately 80 per cent, subsequent recovery does not become complete, and the extent to which it does occur is more closely dependent in degree and time upon the amount of prior fall in cochlear response than upon the oxygen level in the arterial blood during hypoxia. These considerations make it reasonable to suggest either two different stages of damage to the mechanism underlying cochlear microphonics or two mechanisms which are not equally susceptible to interference with their supply of oxygen (see references 6 and 10).

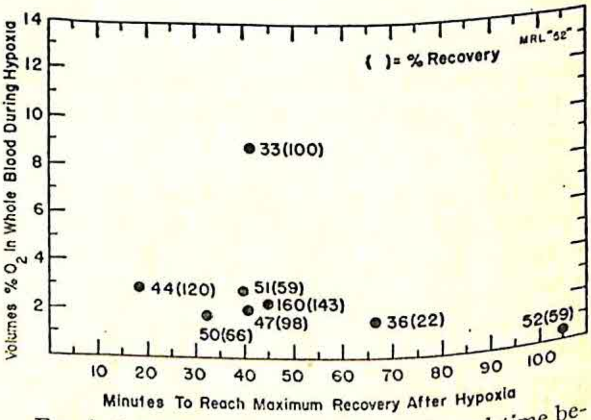

FIG. 4. Arterial oxygen during hypoxia and time before maximum posthypoxic recovery of microphonics

Latency of response to oxygen after hypoxia. We have observed minimal latencies of 20 to 30 sec. between onset of hypoxia and reduction in microphonics. Since our procedure makes it unnecessary for us to allow time for the tube from resuscitator to animal to become washed out with the gas being used, we consider this to be in agreement with the observations of Wever, Lawrence, Hemphill, and Straut (12, p. 206) in setting the uppermost limits to the interval needed for hypoxia to affect the electrical output from the cochlea. That the latency of response to termination of hypoxia can be appreciably less than this is shown by more crucial data obtained from a portion of the posthypoxia recovery curve of cat 41, which deals with the speed of reaction to small amounts of oxygen (Fig. 5). This animal passed through 91 min. with an arterial oxygen level measured at 2.5 vol. per cent and required the use of the resuscitator with compressed air to re-establish spontaneous breathing afterward. Before unaided respiration was fully restored, the effects of single breaths upon a markedly depressed cochlear response were noted. Our protocols reveal that a rise in arterial oxygen content may require no more than 8 to 9 sec. to be reflected beyond dispute in the level of cochlear response. As did Wever *et al.* (12), we must consider the time needed for exchanging air in the alveoli with each breath and for the circulation of oxygenated blood from lungs to cochlea. When this is done, we may hazard a guess that oxygen is almost immediately able to counteract significantly the effects of its deficiency upon cochlear microphonics when excessive damage to the underlying structures is not present. These observations serve to emphasize the smallness of the reserves of energy and material necessary for the metabolic activities directly underlying the microphonics (12).

Significance of Pulse Rate in the Relationship between Adjustments to Hypoxia and Cochlear Response

The conditions governing cardiac rate, stroke volume, venous return, and vasomotor tone are sufficiently numerous and complex to render it impossible to make valid inferences concerning circulation in any portion of the body from a knowledge of pulse rate alone. Electrocardiograms were recorded during most of the work with each animal. Cardiac rates obtained at times showed gross correspondence between directions of change in microphonics and pulse rate, but the changes in pulse often *followed* similar alterations in cochlear response.

Effects of Changes in Arterial Carbon Dioxide upon Cochlear Microphonics

Because we were primarily interested in the effects of hypoxia upon cochlear response, our observations dealing with carbon dioxide were only exploratory. Cochlear microphonics were found to be reversibly depressed, as a result of exposure for periods up to 30 min., by carbon dioxide in concentrations which are within the range of those sometimes used for experimental purposes with man. The diminution tends to increase with greater concentrations of CO_2. Figure 6 shows the response of cats 31, 35, and 48 to mixtures ranging from 5.2 to 25 per cent CO_2 in O_2 or air. The values given with the top and bottom curves (cats 35 and 31, respectively) refer to arterial gas concentrations when the animals were not breathing room air. Cat 35 was given only 5.2 per cent CO_2 in O_2, and cat 31 received 25 per cent CO_2 in air. Values for arterial CO_2 and O_2 were not obtained for cat 48, and the figures accompanying its graph refer to the percentages of CO_2 in O_2 used, these being, in order, 6.7, 6.7, and 24. We should like to call attention to the fact that the values for arterial CO_2 obtained with cat 35 during the administration of CO_2 (40.2 and 32.3 vol. per cent) were of the order of magnitude of those frequently found when the effects of hypoxia upon our cats were being studied, especially while the animals were breathing room air. It should also be noted that the effects of CO_2 are not simple. For example, this gas may act as an anesthetic, a stimulant for certain reflex functions, a vasodilator, and a regulator of pH with secondary

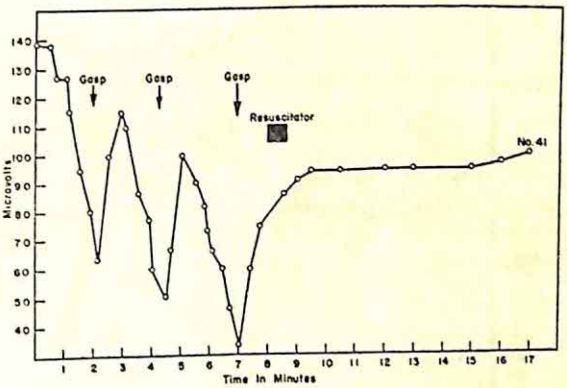

FIG. 5. Effects of single respirations upon microphonics depressed by hypoxia

effects upon electrical conductivity through tissues. By means of the above presentation, we wish primarily to emphasize the need for detailed study of the effects of CO_2 on cochlear function and the importance of considering these effects while focusing attention upon the action of other gases.

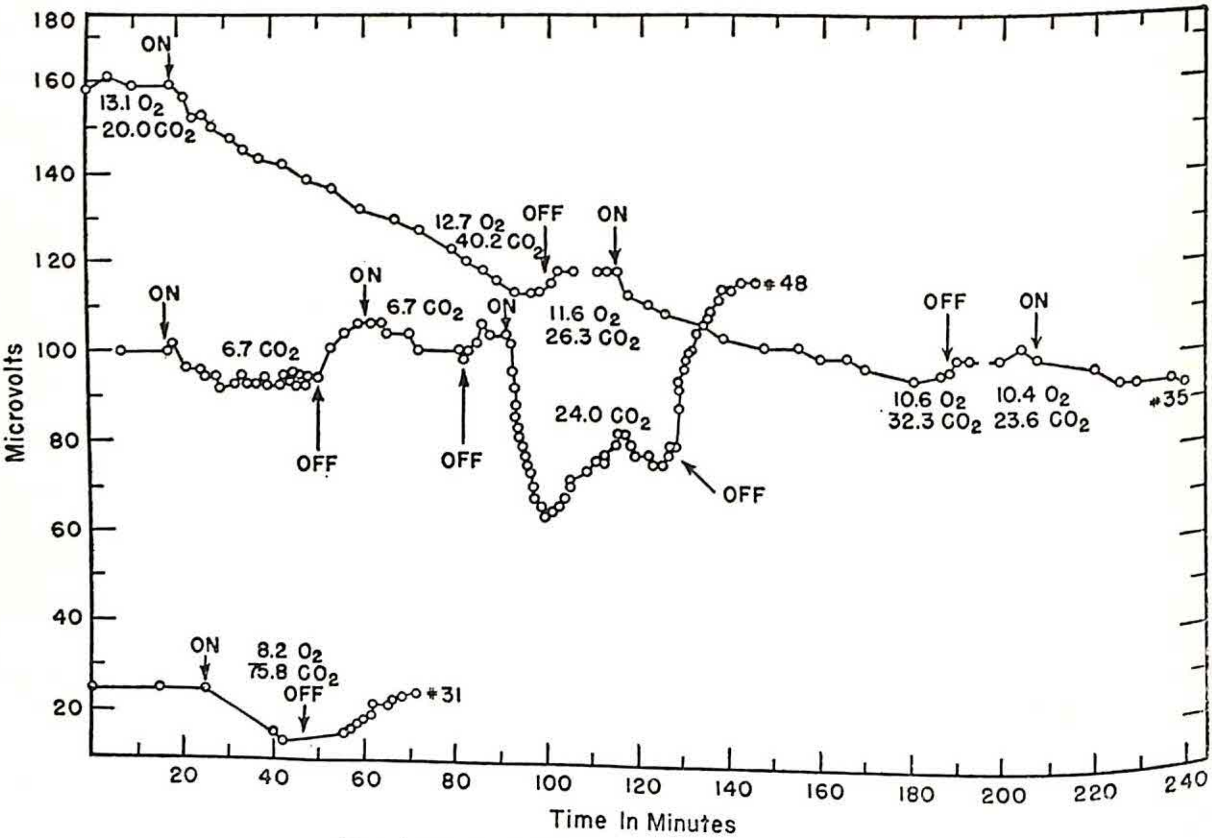

FIG. 6. Effects of CO_2 upon cochlear microphonics

DISCUSSION

In agreement with other studies, a few of which have been cited, our observations indicate that an aerobic metabolic process is basic to the production of cochlear microphonics. The promptness of the change in microphonic level upon the induction of severe hypoxia and especially the demonstrably brief latency of rise in cochlear response following subsequent presentation of oxygen emphasize the closeness of the association between this aerobic reaction (or reactions) and the recorded energy. Our findings may therefore be regarded as further evidence that the ear is not a passive transducing mechanism. Because the anatomy of the inner ear and associated structures has thus far rendered impossible even an approach to precise regulation of substances reaching and leaving the cochlea, we must vary on a grosser scale the chemistry of the organism as a whole and rely upon careful measurements of these changes if we wish to refine our metabolic studies of cochlear activity much beyond recording the effects of directly applied chemicals or of respired gases according to their concentrations. Our data show that cochlear microphonics may be depressed by degrees of hypoxia which are probably mild enough often to permit compensation in full by the adjustive mechanisms of a healthy animal. Thus, again is stressed the intimacy of relation between cochlear response and oxygen. Unfortunately, not enough appears to be known concerning the blood of cats to permit integration of our results with human respiratory physiology at this time. The effects of CO_2 reveal it to be an important and probably too often neglected variable in its own right in physiological studies of auditory mechanisms.

SUMMARY

1. In some cats, reduction of arterial oxygen from an average maximum possible value of 14.1 vol. per cent to 6 to 9 vol. per cent was accompanied by definite though reversible depressions in microphonics.

2. Variability among cats was considerable with regard to the effectiveness of the less severe degrees of hypoxia in reducing microphonics. In this connection, the possible significance of circulatory adjustments and of incidental changes in arterial CO_2 was mentioned.

3. The percentage fall in microphonics during hypoxia was unrelated to the initial amount of cochlear response at the moderate levels elicited in this study.

4. Complete recovery of microphonic output followed arterial oxygen concentrations as low as 2 to 3 vol. per cent maintained for as long as approximately ½ hr. No instance of complete recovery followed hypoxia of sufficient severity to lower arterial oxygen significantly below 2 vol. per cent.

5. When arterial oxygen was below about 3 vol. per cent, the lower the level of arterial oxygen, the longer was the time required to reach maximum recovery.

6. When the decline in microphonics during hypoxia exceeded 80 per cent, subsequent recovery upon termination of hypoxia was reduced and its temporal course was greatly prolonged.

7. No more than 8 to 9 sec. need elapse between the inhalation of oxygen in room air and a significant increase in microphonics already depressed by hypoxia.

8. Cochlear microphonics were reversibly reduced by inspired CO_2 in O_2 (or air) in concentrations between 5.2 per cent and 25 per cent.

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BEHAVIORAL ADJUSTMENT TO THIAMINE DEFICIENCY IN ALBINO RATS[1]

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Animals deficient in thiamine have been reported to increase their intake of the needed vitamin when thiamine is available. Among biochemists a simple effect theory has gained credence to explain vitamin selection. This explanation accords a central role to the animals' "feeling of well being" which is said to lead to an increased intake of the reinforcing substance. If the time of increased intake of a needed vitamin is a function of the animal's response to internal changes associated with approach toward some physiological optimum, then the increase in rate of intake is likely to occur, in the case of thiamine, about 1 hr. after ingestion of some thiamine. Reaction to the ingestion of thiamine by a deficient animal occurs within the first hour after intake. Marked physiological and chemical changes occur during this short time.

Scott and Quint (2) report an experiment in which rats deficient in thiamine, given a choice for a three-week period of food lacking and food including thiamine, all chose the thiamine-containing diet almost exclusively on the first or second day. It is not possible from this experiment to conclude with accuracy when the animals increase their rate of thiamine intake. For this purpose, the Skinner-box experiment described below was designed.

The papers of Scott and Quint (2) and of Scott and Verney (3) support the notion that thiamine-deficient animals make choices which solve their deficiencies. Their papers leave open one question. Control animals eat about as much thiamine-containing food during a three-week control period as thiamine-deficient animals eat during a three-week experimental period. This is to say, significant differences in intake of thiamine by deficient rats may be a function of the control group's decrease in intake of thiamine with prolonged contact with it. To conclude that the deficient animals are behaving adaptively would first require control of the habituation factor. To this end, the free intake experiment described below was undertaken.

A recent advance in biochemistry permits us to use a short cut to create thiamine deficiency. Frohman and Day (1) report that an analogue of thiamine, oxythiamine, is capable of replacing thiamine in animal tissues and, in addition, causes excretion of body thiamine in weanling rats. Within 12 hr. after intraperitoneal injection of oxythiamine, Frohman and Day report that extreme nervousness and incoordination are observed. In the experiment to be reported, thiamine-free diet and oxythiamine were used to produce avitaminosis.

EXPERIMENT I

Procedure and Apparatus

Sixty-four male albino rats, 30 days of age (±5 days), were habituated to handling for 3 days and then given training to the click of a magazine for 2 days. Magazine training and subsequent bar-pressing training were performed when animals were deprived of water for 22 hr. Reinforcement was a drop of distilled water (.02 to .03 cc.). Conditioning was spaced over 4 days. A total of 300 reinforcements was allowed. In practice, the total number of reinforcements varied from 289 to 312. Any discrepancy of more than 5 per cent in total number of reinforcements caused an animal to be eliminated. Since eight animals were bar pressing during every run, and since the counters were in a room apart from the Skinner boxes, *E* was not always able to remove an animal immediately following the three-hundredth response.

Following the four conditioning runs, the entire group was divided randomly into an experimental and a control group. All animals were weighed, and the two groups were found to differ in average weight by only 1 gm.; the mean weight for the experimental group was 77 gm., for the control group 76 gm. Two days after weighing, the control group was given an intraperitoneal injection of 40 micrograms of thiamine in 1 cc. of saline; the experimental group received 1 cc. of saline. Five days later, all animals were weighed; since no differences between group weights appeared after seven more days, the dose of thiamine was increased to 250 micrograms for the control group. Saline alone was administered to the experimental group. Three days later differences in the rate of gain between the two groups began to appear.

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[1] This report is based upon a dissertation submitted to Indiana University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The writer is indebted to Dr. R. C. Davis for his generous advice and criticism and to Drs. C. J. Burke and W. S. Verplanck for their help in planning the design and statistical analysis. The writer is indebted also to Dr. H. G. Day for advice on the chemistry of thiamine deficiency. This work was made possible by a grant from the Graduate School of Indiana University. Dr. P. T. Young kindly read and criticized the manuscript.

[2] Now at the University of Illinois.

For the test run four control animals and four experimental animals were run in the Skinner box during each 48-hr. period following the first appearance of differences in rate of weight gain. No experimental animal was run if its weight gain exceeded 11 gm. from the time of the first weighing.

All animals were run in the Skinner box under low thirst drive. The animals were deprived of water for a 16-hr. period, from 5 P.M. to 9.A.M, watered for 1 hr., and run 5 hr. after removal of water. The Skinner box contained a thiamine solution of .0025 per cent, a drop of which served as reinforcement for every bar-pressing response. The reinforcing solution contained 25 micrograms of thiamine in 1 cc. of distilled water; 25 micrograms is the approximate daily thiamine requirement for rats of this age.

The animals were permitted to press the bar until satiated. The criterion for satiation was 15 min. of no responding *after* the animal had made some responses. Usually this was accomplished within 1 hr. Following satiation, all cages were opened and two dishes, one containing thiamine-free food and the other containing distilled water, were placed in a corner of the cage. The animals were kept in the Skinner box for 46 hr. All bar presses were recorded. The number of rats run through the whole experiment was 41, 22 in the control group and 19 in the experimental. Rats were eliminated before testing in the Skinner box for failure to condition within the allotted time, failure to fulfill the weight requirements, for any failure of the Skinner-box apparatus, and for any continued illness.

Animals were maintained in the Skinner box for a 46-hr. period at a temperature slightly higher than room temperature. This temperature difference was due to heating by the rat itself and by the light in the apparatus. Air change was maintained by a suction pump which was connected by rubber tubing to all cages through a negative pressure manifold operated by a mechanical vacuum pump. This pump sucked out air, which caused fresh air to enter through small holes in the side of the box. This functioned as air cooler, ventilator, and deodorizer of the box.

Results

Figure 1 shows the rates of bar-pressing responses for experimental and control groups. The experimental group gives more responses in the Skinner box than does the control group. The difference between the two groups appears within the first 18 hr., and thereafter differences are negligible. The initial difference in average number of responses (45.1) made by both groups during the 1-hr. satiation period yields a value of 3.8 on the Mann-Whitney test, significant well beyond the .01 level.

An attempt was made to correlate frequency of response with some measure of activity. Ten animals in each group were run through an activity wheel which mechanically recorded the number of revolutions they ran in 1 hr. The control group gave an activity score average of 113.5 revolutions while the experimental group gave only 102.1. No support can be said to be given to a simple activity correlate, although these data are not reliable enough to rule out the correlation even for our group of animals.

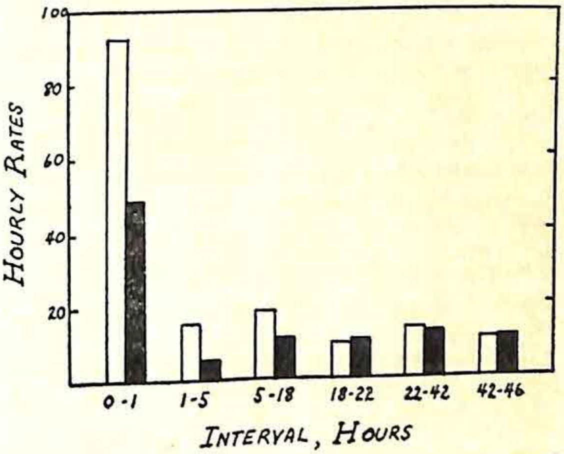

FIG. 1. Hourly rates of responding of experimental and control animals for six time samples during 46 hr. in the Skinner box. White bar = experimental group; black bar = control group.

EXPERIMENT II

Procedure and Apparatus

Fifty male albino rats, averaging 30 days of age (±5 days), were habituated for 2 days to a thiamine-free diet. Following these 2 days, two groups of 25 animals were selected by means of a table of random numbers and designated as experimental and control groups.

The two groups of 25 rats were broken down further into five subgroups for five concentrations of thiamine solution. These subgroups were given 4 days in the experimental cages with a choice between a single concentration of a solution of thiamine hydrochloride and distilled water. The thiamine-free food was available at all times for these four days. After each 24 hr. the liquid removed by the animals from the bottles was measured. The position of the two bottles for a single animal remained constant throughout the experiment. For any group of rats subjected to a given concentration, five had thiamine on the right and five had thiamine on the left side.

After 4 days in the experimental cages, all animals were removed to home cages and left on a thiamine-free diet for 19 days and given intraperitoneal injections. The control group received 250 micrograms of thiamine in 2 cc. of saline; the experimental group received 200 micrograms of oxythiamine in 2 cc. of saline.

Forty-eight hours after these injections, the animals were returned to the experimental cages for 4 days under the same conditions of choice as existed during the control period. Thus, we have group variations due to treatment (oxythiamine vs. thiamine), concentration, and days.

The measurement of intake requires some description. At the same time every day on days 3 to 6 inclusive and days 9 to 12 inclusive, all bottles were removed from the cages and measurements were taken. All water bottles were handled first; then, in order of increasing concentration, all bottles with thiamine were handled. Measurement was made as follows: all bottles were refilled from a 10-cc. pipette graduated in .1 cc. (with whatever solution they already contained) until the liquid reached the 30-cc. mark on the bottle.

The highest concentration (called concentration 5 hereafter) was a .25 per cent solution of thiamine (.25 gm. of thiamine in 100 cc. of distilled water). The concentrations 4, 3, 2, and 1 were successively weaker by single log units (.025 per cent, .0025 per cent, .00025 per cent, and .000025 per cent). The solutions were prepared by the dilution method. These five concentrations were used since preliminary trials indicated almost no intake of thiamine beyond the .25 per cent level.

The rats were kept on wire mesh above reach of the pans for droppings. No rat was able, under these conditions, to reach his feces. This control was necessary since deficient animals are able to make up deficiencies in diet by eating their feces.

The intake cages measured 8¾ in. deep by 10 in. long by 7⅞ in. wide. Choice bottles were kept flat against the wire mesh at the side of the cage by means of metal hooks which held an elastic band behind the two bottles. This arrangement kept the position of the tubes stable. The hole through which the animals drank was in the low point of a J-shaped tube. Leakage from the tip was eliminated in this way.

Results

The results show that rats, like humans (unpublished study, P. T. Young), prefer water to thiamine solution. This is true for both experimental and control groups. Comparison of preferences before and after the injections indicates that 17 of 25 experimental animals showed increased preference for water and 21 of the 25 control animals showed the same trend. The difference between the preferences observed and an expectation of randomness yields a chi square significant at better than the .01 level.

Table 1 demonstrates the trend toward decreased intake in cubic centimeters of thiamine solution as the concentration of the thiamine solution increases by successive log units. Table 1 is based on data for ten animals, five in the control, five in the experimental groups. This combining of groups is valid, since the animals have had no differential treatment yet. In preliminary tests on four pairs of animals, using our concentration 3 and moving successively higher up to 1 per cent, a marked decrease in intake occurred.

TABLE 1
Average Intake of Thiamine for Four-Day Period for Five Concentrations of Thiamine

CONCENTRATION	INTAKE, IN CC.
1	16.67
2	19.01
3	16.53
4	11.50
5	5.23

TABLE 2
Ratio of Thiamine Intake to Total Fluid Intake for All Concentrations

	CONCENTRATION	EXPERIMENTAL GROUP	CONTROL GROUP
Before injection	1	0.45	0.68
	2	0.54	0.65
	3	0.44	0.50
	4	0.37	0.39
	5	0.15	0.17
	Mean	0.39	0.48
After injection	1	0.56	0.53
	2	0.49	0.37
	3	0.31	0.39
	4	0.39	0.35
	5	0.15	0.09
	Mean	0.38	0.35

Table 2 shows our intake figures converted into ratios of thiamine intake in cubic centimeters over total fluid intake. This analysis suggests that the nondeficient animals tended to choose proportionally less thiamine in their total fluid intake with extended contact with thiamine as a choice (13 per cent less), while deficient animals maintained their thiamine intake. No optimum concentration for thiamine intake could be established.

While no significant treatment effect was found, an analysis of variance for an interaction effect of treatment and concentration was highly significant. The *F* for concentration by treatment was 23.382 with 4 and 40 *df*, significant at better than the .01 level.

This result indicates that any specifically adaptive increase in intake of thiamine due to deficiency is connected closely with the concentration of thiamine offered. In the light of this statistical result, we may note that the experimental group begins to take consistently more thiamine than does the control group at our two highest concentrations.

Table 3 shows the difference in intake of the five concentrations between the experimental period (after injections) and the control period (before injections) for both groups. The difference between the experimental and control groups in the two highest concentration groups is more reliable from day to day and for concentration 5 is proportionally a much larger difference, since the intake of thiamine is already so low. Animals in the subgroups for concentration 5 show the most stable water and thiamine preferences of all five groups.

TABLE 3

Average Differences between Intake in Cubic Centimeters of Thiamine for Four-Day Period before and after Injections (Postinjection Intake Minus Preinjection Intake)

CONCENTRATION	EXPERIMENTAL GROUP	CONTROL GROUP	EXPERIMENTAL — CONTROL
1	2.65	3.80	−1.15
2	11.94	−3.75	15.69
3	0.94	6.10	−5.16
4	10.54	8.86	1.68
5	4.60	−0.62	5.22
Mean	6.13	2.88	3.26

DISCUSSION

The results suggest that intake of thiamine, unlike that of sucrose and salt, exhibits no concentration of optimum intake. When discriminated from water, thiamine seems to be less preferred; then, as thiamine concentration increases, rats take less and less.

While our experiments differ somewhat from those of Scott and his co-workers, an examination of the data of Scott and Verney shows much in common with our data. Although our concentrations cannot be equated, since they used thiamine mixed in food and we used it in solution, still their deficient animals surpassed their control animals, as in our results, *only* at the higher concentrations; Scott and Verney's control animals, like ours, decreased their thiamine intake with prolonged contact with thiamine. Our results indicate that deficient animals do not show this decrease in intake even when habituation is controlled.

Our results do not show that deficient animals drink exclusively from the thiamine bottle after 1 to 2 days of contact with thiamine. Scott and Quint report such selective behavior for their thiamine-food mixture. We were unable to find any significant trend effects with time in our free-intake experiment.

The significant concentration by treatment interaction found in the intake experiment suggests that taste and/or immediacy of effect may be operative since discrimination of thiamine and biological response are enhanced at higher concentrations. The effect of heightened activity during deficiency cannot account alone for such an interaction.

The results in the Skinner-box experiment using a thiamine concentration of .0025 per cent (concentration 2 of the intake experiment) are difficult to interpret in accord with any single theory available. The rate of bar pressing by deficient animals surpasses the rate of the control animals within the first hour. Barring the very unlikely notion that deficient animals take more fluid than do healthy animals, we are forced to conclude that the learned "effect" of thiamine intake occurs more quickly than the earliest measured physiological effects of thiamine. This is not impossible, but it is somewhat disquieting. Despite the results in the activity wheel referred to above, the author does not wish to rule out the parsimonious hypothesis of increased activity in deficiency suggested by Wald and Jackson (4). Higher activity rates of deficient animals could produce the results we obtained in the Skinner-box experiment. Our own activity wheel results, for a sample of 20 animals, do not confirm this hypothesis, but are not sufficiently reliable to eliminate the activity hypothesis as an explanation.

SUMMARY AND CONCLUSIONS

Two experiments are described, a Skinner-box and a "free-intake" experiment. In both experiments the behavior of rats deficient in thiamine is compared with the behavior of normal rats in the presence of thiamine.

The Skinner-box experiment with thiamine solution as reinforcement results in more responses by deficient rats than by normal rats. This difference appears to be significant during the first hour in the Skinner box, and thereafter the rates of the two groups tend to merge. The immediacy of the effect suggests that activity-level differences alone might account for this result. The inadequacy of activity level as a full explanation, however, is noted for free-intake phenomena.

Under free-intake conditions, offering a choice of distilled water and one of five thiamine concentrations in solutions, the following results are obtained:

1. Rats generally prefer water to thiamine when the thiamine concentration is .0025 per cent or greater. With increasing contact with thiamine, the preference becomes more marked and extends to lower concentrations.

2. Independent of need for thiamine, the curve of thiamine intake shows decline in absolute intake of thiamine with increase in concentration.

3. Statistical analysis of thiamine-intake figures at thiamine concentrations .25, .025, .0025, .00025, and .000025 per cent indicate: (*a*) there is no simple effect of thiamine deficiency on thiamine intake; (*b*) there is no significant difference in temporal pattern of thiamine intake with habituation by deficient and normal rats; and (*c*) there is a significant interaction effect of nutritional condition and thiamine concentration on intake of thiamine which seems to appear at our two highest concentrations.

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THE EFFECT OF AUDIOGENIC CONVULSIONS ON A CONDITIONED EMOTIONAL RESPONSE

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Previous research by Hunt and Brady (1, 2) has demonstrated that a conditioned emotional response (CER) of the "fear" or "anxiety" type can be virtually eliminated or markedly reduced in strength by a series of 21 electroconvulsive shocks (ECS). This effect of ECS upon the CER is markedly attenuated, however, when the convulsion is prevented by ether anesthesia just before administration of the electroshock treatment (4). This finding points to the convulsion as a necessary condition for reducing the strength of the CER. The present experiment investigates the possibility that the convulsion alone without electroshock may be a sufficient condition for reducing the strength of the CER. Specifically, the present experiment tests the effect of a series of audiogenic convulsions upon the retention of a previously conditioned emotional response.

METHOD

Subjects

Eighteen male albino rats, 60 days old at the beginning of the experiment, served as *S*s.

Emotional Conditioning Procedure

The CER was established in Skinner boxes according to the procedure previously described by Hunt and Brady (2). In brief, the animals were first trained to produce a stable output of lever-pressing responses for an aperiodic water reward. Every animal then received six emotional conditioning trials, each consisting of a 3-min. presentation of a clicking noise (the conditioned stimulus) terminated contiguously with two momentary painful electric shocks (approximately 1.5 ma.) to the feet (unconditioned stimulus), delivered through the grill floor of the apparatus. Most of these conditioning trials were spaced several days apart, with adaptation runs intervening; only one trial was given on any one day in order to minimize the development of generalized fear reactions to the apparatus. Records were kept of the lever-pressing output for the first, second, and third 3-min. segments of the daily 9-min. lever-pressing trials. For all conditioning and retention tests, the clicker was introduced at the beginning of the fourth minute, and the unconditioned shock stimulus, if given, was introduced at the end of the sixth minute when the clicker was turned off. The conditioned emotional response in this situation develops as a marked reduction or complete cessation in lever pressing, usually accompanied by defecation, during presentation of the clicker.

Audiogenic Seizure Procedure

Twenty-four hours after the sixth emotional conditioning trial, the auditory stimulus was presented for the first time to each animal. The *S*s were housed in a small metal box (9 in. by 6 in. by 5 in.) with a hardware-cloth top. The box was fastened an inch or so beneath a row of small, hard steel strips cut to resemble keys and suspended by steel wires from a steel bar measuring 7 in. by 1 in. by ⅛ in. This bar and "key" assembly, driven back and forth by a 1⁄12-hp, 1745-rpm electric motor, produced an intense auditory stimulus resembling "jingling keys." Each animal was subjected to 2 min. of such stimulation on each trial.

Beginning on the day following the last emotional conditioning trial, and continuing for 42 days, all 18 animals received auditory stimulation once every other day. Then, 4 days after completion of this initial series of 21 exposures, all animals received stimulation once every day for 15 additional days, giving a total of 36 exposures. The incidence of full-blown tonic-clonic convulsions and/or running fits produced by these exposures was recorded for each animal.

Retention Test Procedure

On the third day after completion of the first series of 21 exposures to the key-jingling stimulus, all animals were tested for retention of the conditioned emotional response by a single unreinforced presentation of the clicker stimulus during the daily Skinner-box run (test 1). Then, on the third day after completion of the second series of 15 exposures a second retention test was conducted (test 2).

All animals were maintained on a 23-hr. water deprivation schedule during both conditioning and retention test periods, but had free access to food and water in their home cages during the audiogenic stimulation period.

RESULTS

For purposes of convenience in summarizing the results of this experiment, the 18 animals have been separated into three groups based upon the number of convulsions induced during the experiment. In group I (4 animals), all animals had 30 or more convulsions. In group II (10 animals), no animal had more than 26 or less than 1 convulsion. And in group III (4 animals) no animal had any convulsions.

Table 1 shows the course of the CER and the incidence of audiogenic convulsions for each of the three groups throughout the critical stages of the experiment. The "inflection ratio" in columns 1, 2, 4, and 7 is the only measure that requires explanation. It indicates how much and in which direction the clicker, during the second 3 min. of the trial, changes the output of lever responses (see reference 3 for a more complete discussion). It expresses the difference in output between the first and second 3-min. segments of the lever-pressing curve as a fraction (percentage in decimal form) of the output during the first 3-min. segment. (The inflection ratio is expressed by the formula $\frac{B - A}{A}$, where A is the number of lever responses made during the first, and B is the number made during the second 3-min. segment of the curve.) Complete cessation of lever pressing during the clicker (or second 3 min. of the curve) would appear as a ratio of −1.00, essentially unchanged output as a ratio of around 0.00, and a 100 per cent increase as a ratio of +1.00.

TABLE 1

The Effect of Audiogenic Convulsions on the Conditioned Emotional Response in Groups I, II, and III

	1	2	3	4	5	6	7
GROUP NO.	1ST EMOTIONAL CONDITIONING TRIAL	6TH EMOTIONAL CONDITIONING TRIAL	ALTERNATE DAY AUDIOGENIC SERIES (42 days)	1ST RETENTION TEST	DAILY AUDIOGENIC SERIES (15 days)	TOTAL AUDIOGENIC SERIES	2ND RETENTION TEST
	Mean Inflection Ratios	Mean Inflection Ratios	Mean Number of Convulsions	Mean Inflection Ratios	Mean Number of Convulsions	Mean Number of Convulsions	Mean Inflection Ratios
I	+.06	−1.00	20	−.93	13	33	+.08
II	+.03	−1.00	8	−.96	5	13	−.39
III	+.01	−1.00	0	−.98	0	0	−.97

The sharp drop from values around 0.00 (col. 1, Table 1) to a value of −1.00 (col. 2, Table 1) between the first and sixth conditioning trials reflects the development of the CER in all three groups. A concurrent increase in the stool count, taken during the 3-min. clicker presentation between the first and sixth conditioning trials also reflects this conditioning. Column 3 shows the incidence of convulsions for each of the three groups during the 42-day series of alternate-day audiogenic stimulus exposure. Inspection of the data for all 18 animals revealed a complete spectrum of susceptibility; some animals in group I convulsed on almost every exposure, while others in group III never had convulsions under any circumstances. Column 4 shows the results of the first retention test; all three groups retained a very strong CER. Apparently, this first series of 21 audiogenic exposures produced no significant change in the strength of the CER in any of the three groups.

Column 5 shows the incidence of convulsions in all three groups during the second series of 15 daily exposures to the audiogenic stimulus. Again, the same spectral pattern of susceptibility observed during the first series of audiogenic exposures was apparent upon inspection of the data for all 18 animals. Column 6 shows the sum total of convulsions for all three groups on both the initial (alternate-day) and the second (daily) series of audiogenic exposures. The spectrum of susceptibility was again clearly evident, with the animals in group I showing 30 or more full-blown tonic-clonic convulsions and the animals in group III showing neither a convulsion nor a running fit on any occasion throughout the experiment.

In Column 7, the results of the second retention test are shown. For the animals of group I, both the inflection ratios and stool counts indicate virtual elimination of the CER. A marked reduction in the strength of the CER is also apparent in group II, and this reduction is directly related to the incidence of audiogenic convulsions. Finally, no change in the strength of the CER can be observed in the animals of group III.

A rank-order correlation analysis of the magnitude of the decrease in the inflection ratio between test 1 and test 2 for each of the 18 animals and the total number of audiogenic convulsions for each of the 18 animals, yields a coefficient of +.89. In addition, a rank-order correlation coefficient of +.85 was obtained between the number of audiogenic convulsions for each of the 18 animals during the second series of daily exposures and the decrease in the magnitude of the inflection ratio for each of the 18 animals between test 1 and test 2. Both correlation coefficients are highly significant (.01 level of confidence). The distribution of stools throughout the groups on these tests also tends to confirm the direction of this change in the strength of the CER.

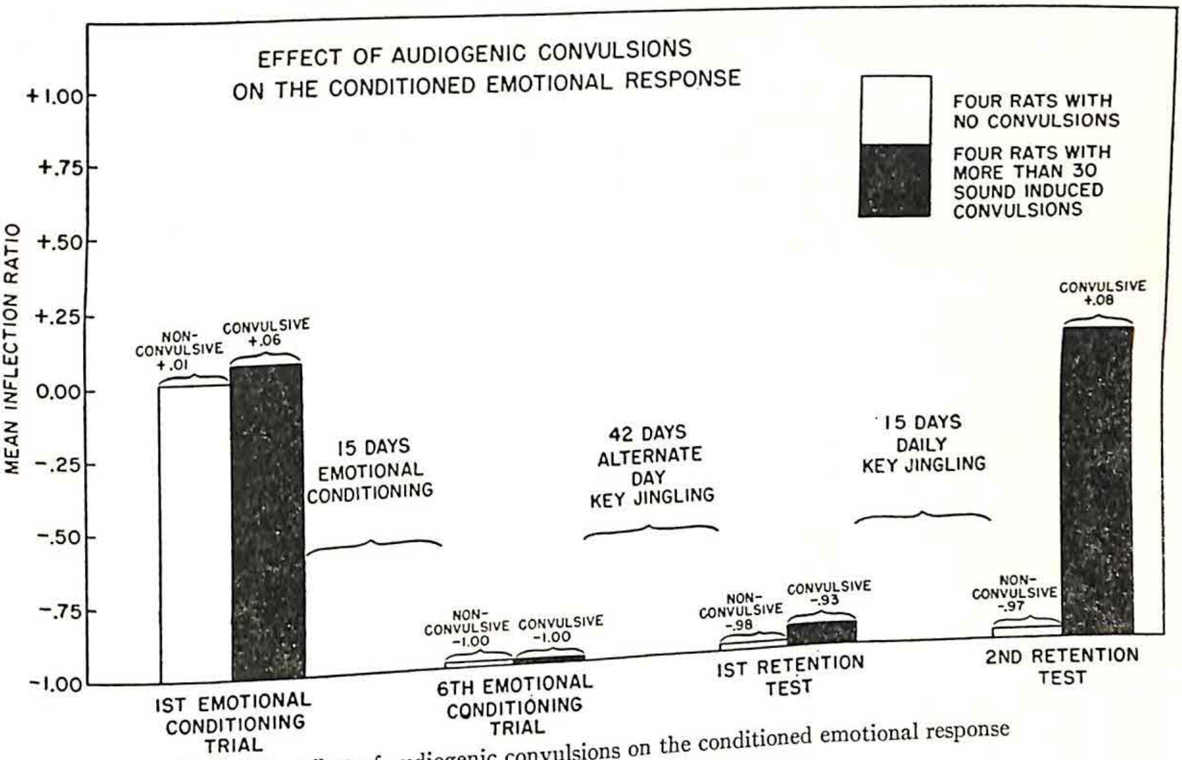

FIG. 1. The effect of audiogenic convulsions on the conditioned emotional response

Figure 1 represents in graphic form the results obtained by comparing mean inflection ratios throughout the critical stages of the experiment for the four animals with 30 or more convulsions (group I) and the four animals with no convulsions (group III). It will be seen that there is no significant difference between these two groups of animals up through the first retention test. The decrease in the strength of the CER on the second retention test for the group with 30 or more convulsions is highly significant, however (.01 level of confidence).

DISCUSSION AND CONCLUSIONS

The results of this experiment indicate quite clearly that a series of audiogenic convulsions can have the immediate effect of diminishing, or virtually eliminating, a conditioned emotional response established prior to the convulsive experience. The essential similarity between these changes in the CER and those following electroconvulsive shock (1, 2) suggests that some event, or events, related to the convulsive process per se is sufficient to attenuate or abolish the conditioned emotional response. In addition, the finding that electroshock alone without convulsion (4) and that auditory stimulation alone (*vide supra*) produce little if any change in the CER would seem to indicate that the convulsion may be characterized as both a necessary and sufficient condition for reducing the strength of the CER. The main point, however, is clear: convulsions of two different origins can produce essentially the same effect upon the conditioned emotional response.

The results of this experiment, however, are not completely consistent with the reported effects of electroconvulsive shock upon the conditioned emotional response. The ECS experiments (1, 2) have indicated quite clearly that a series of 21 electrically induced convulsions is sufficient to produce a significant reduction in the strength of the CER. In the present experiment, however, the initial series of up to 21 audiogenic convulsions produced little or no significant change in the strength of the CER (see col. 3 and 4, Table 1 above).

At least two possible explanations for this discrepancy present themselves. First, it may be that the audiogenic convulsions are less potent than the ECS convulsions so that their effect does not appear unless the CER is weak enough to be at a critical threshold value for the given amount of treatment. The data of this experiment could be accounted for within this framework by assuming that the first 21 audiogenic exposures, plus the one extinction trial of test 1, weakened the CER to such an extent that the second series of convulsions could virtually eliminate the response. A second possible explanation would be that the temporal distribution of the convulsive treatments may constitute a critical factor in producing the change in the CER. In the ECS experiments, the 21 convulsions were induced over a 7-day period, requiring the administration of 3 treatments per day. In the present experiment, the first 21 convulsions were induced over a 42-day period, 1 every other day. Within the framework of this second explanation, the reduction in the strength of the CER following the complete series of audiogenic convulsions in the present experiment would be accounted for by the change from the less intensive schedule of 1 treatment every other day for 42 days to the more intensive regimen of 1 treatment per day for 15 days.

In order to provide some information as to which of these two possible explanations best accounts for the data, a control experiment was performed. The conditioned emotional response was established in six rats according to precisely the same procedure followed in the main experiment. Twenty-four hours after the sixth conditioning trial, all animals began a series of 21 electroconvulsive shock treatments administered 1 every other day for 42 days. Although some diminution in the strength of the CER was apparent in three of the six animals during a retention test conducted on the third day after completion of the treatments, a strong response survived the 21 convulsions in all animals (the mean inflection ratio for the group on this retention test was −.90).

The results of this control experiment indicate quite clearly that a series of 21 ECS treatments administered on alternate days over a 42-day period produces considerably less effect upon the CER than the same series of 21 treatments concentrated in a 7-day period. Thus, it would appear that the discrepancy between the results obtained with 21 audiogenic convulsions and those reported with 21 ECS convulsions may well be accounted for in terms of the difference in temporal distribution of the treatments without positing any essential difference in the potency of ECS and audiogenic convulsions.

SUMMARY

The present experiment investigates the effects of a series of audiogenic convulsions on a conditioned emotional response of the "fear" or "anxiety" type. After the emotional response had been established in 18 male albino rats, all animals received 36 2-min. exposures to an intense auditory "key-jingling" stimulus. Retention tests following these exposures revealed virtual elimination of the conditioned emotional response in those animals showing a high incidence of convulsive reactions to the audiogenic stimulation. In contrast, those animals which did not convulse in response to the "key-jingling" stimulation at any time during the experiment showed complete retention of the conditioned emotional response.

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THE EFFECT OF ELECTROCONVULSIVE SHOCK (ECS) ON A CONDITIONED EMOTIONAL RESPONSE: THE EFFECT OF ADDITIONAL ECS CONVULSIONS

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Earlier experiments in this series have demonstrated that 21 electroconvulsive shocks (ECS), given 3 per day for seven days, have the immediate effect of attenuating a conditioned emotional response (CER) of the "anxiety" or "fear" type (3, 5). The attenuating effect of ECS is temporary, however (1). This may be attributable, at least in part, to the dissipation with time of those physiological consequences of the convulsions which are responsible for the attenuation of the CER. But other data suggest that the CER itself increases in symptomatic strength with rest and/or elapsed time (2). Thus, the CER in untreated control animals becomes more resistant to experimental extinction (by nonreinforcement) if the extinction is postponed for a month or more after conditioning. Furthermore, the CER also becomes more resistant to attenuation by ECS if the treatment is similarly postponed.

Changes in the symptomatic strength of the CER with elapsed time and/or rest probably contribute somewhat to the posttreatment recovery of the CER. Post-ECS experimental extinction, which presumably has a direct decremental effect upon the CER itself as a habit, prevents this posttreatment reappearance of the response (6).

The present experiments were intended to determine whether "additional" ECS (ECS$_a$), in an amount which by itself ordinarily has little or no noticeable or immediate effect on the CER, will prevent the posttreatment recovery of the CER (Experiment I) or make the CER less resistant to delayed treatment with a more intensive series of ECS (Experiment II). The "additional" convulsions, unlike experimental extinction, should either augment or prolong the effects of an intensive series of 21 ECS or otherwise prevent the usual posttreatment recovery of the CER. And the "additional" convulsions, if given over a period of days prior to delayed intensive treatment, should counteract the usual increase in symptomatic strength of the CER which normally occurs with time. If so, the more intensive series of 21 ECS given a month or more after conditioning should attenuate the CER in those animals that also received "additional" convulsions.

EXPERIMENT I

The Effect of "Additional" ECS on the Posttreatment Recovery of the CER

Method

Subjects. Thirty naive, male, albino rats, 60 days old at the beginning of the experiment, served as *Ss*.

Emotional conditioning procedure. The conditioned emotional response (CER) was established in Skinner boxes in accordance with our standard procedure (5, 6). In brief, all animals were trained in lever pressing until they showed a stable output of lever responses for an aperiodic water reward. Then all animals received a total of eight emotional conditioning trials, each consisting of a 3-min. presentation of a clicking noise (as the CS) terminated contiguously with two momentary electric shocks to the feet (approximately 1.5 ma.) as the unconditioned stimulus, delivered through the grill floor of the Skinner box. Most of the conditioning runs were spaced several days apart; only one conditioning trial was given on any one day. On the intervening days the animals had "adaptation" runs during which neither the clicker nor the shock was presented. This method minimizes the development of generalized fear reactions to the apparatus and allows the CER to appear more clearly as a plateau or dip in the cumulative curve recording the output of lever-pressing responses. This reduction or cessation in lever pressing during presentation of the CS constitutes the CER; it is usually associated with defecation during that run in the apparatus.

The animals had daily 9-min. runs. A record of the total number of lever responses made by the end of the third, sixth, and ninth minutes of each run by each animal was kept. On conditioning days, the CS was introduced at the beginning of the fourth minute and terminated contiguously with the UCS (shocks at) the end of the sixth. Presentation of the CS alone during the second 3-min. segment of a run tested for retention of the CER after treatment.

The *inflection ratio* (6) describes the magnitude of the CER. Briefly, this ratio expresses the difference in output between the second and first 3-min. segments of the curve—the effect of presentation of the CS upon output of lever responses—as a proportion of the output during the first 3-min. segment. If the CS produces no change in output, the ratio is 0.00; if the animal has a strong CER and makes no lever responses during the CS, the ratio is −1.00; if a strong CER with a ratio of −1.00 or −.90 is attenuated, the ratio shifts in the positive direction toward 0.00; and so on (see 6).

Electroconvulsive shock. The ECS apparatus and procedure were the same as described previously (3, 5). The apparatus delivers 50 to 54 ma. for .18 sec. through moistened electrodes clipped to the ears. Two series of ECS treatments were employed—the main intensive series of 21 ECS, given 3 per day for 7 days, and the "additional" ECS (ECS_a). ECS_a consisted of 15 convulsions given 1 every other day over a period of 30 days, beginning on the fourth day after the completion of the main series and on the day following the first posttreatment retention test (test 1). Animals not receiving a particular treatment series received equivalent pseudo-ECS to control for the effects of handling, pinching the ears, and so forth.

Plan of the experiment. After the eighth emotional conditioning trial, the animals were divided into groups, roughly equated for the strength of the CER as it appeared to develop during the conditioning trials, and treated as follows:

Group I received ECS; a retention test (test 1), ECS_a, and a second retention test (test 2) ($N = 12$).

Group II received ECS, test 1, pseudo-ECS_a, and test 2 ($N = 6$).

Group III received pseudo-ECS, test 1, ECS_a, and test 2 ($N = 6$).

Group IV received pseudo-ECS, test 1, pseudo-ECS_a, test 2 ($N = 6$).

The animals were on a 23-hr. water-deprivation schedule at the time of all conditioning and test trials, with free access to food in the home cages. During the ECS and rest periods, all had free access to both food and water.

All retention tests came on the third day following the last preceding ECS and following one day of adaptation in the Skinner box. Test 1 thus came on the eleventh day after the last conditioning trial. Test 2 came on the forty-third day after the last conditioning trial, on the thirty-fifth day after the last of the main ECS convulsions, and on the thirty-second day after test 1. ECS_a, the "additional" ECS, began on the twelfth day after the last emotional conditioning trial.

Results

Figure 1 shows the mean inflection ratio for each group on conditioning trials 1 and 8 and on both retention tests. The sharp negative shift between trials 1 and 8 reflects the development of the CER as a result of conditioning. The positive shift between trial 8 and test 1 for groups I and II reflects the attenuating effect of the main series of 21 ECS upon the CER. All but 1 of the 18 animals in groups I and II showed a positive shift in the ratio while none of the 12 in groups III and IV departed from a ratio of −1.00; this difference is significant ($\chi^2 = 22.45$, $p < .01$).[1]

The "additional" ECS, by itself, did not attenuate the CER in group III, as measured by test 2. But the contrast between groups I and II in the shifts in inflection ratio between tests 1 and 2 shows the effects of ECS_a when added to the main series of 21 ECS. All animals in group II, which received no ECS_a, showed larger negative inflection ratios on test 2 than on test 1. In contrast, all but two of the animals in group I, which did receive ECS_a in addition to the regular treatment, showed shifts in the inflection ratio in the positive direction. This difference is significant ($\chi^2 = 8.13$, $p < .01$) and indicates that the "additional" ECS acted to prevent the post-ECS recovery of the CER.

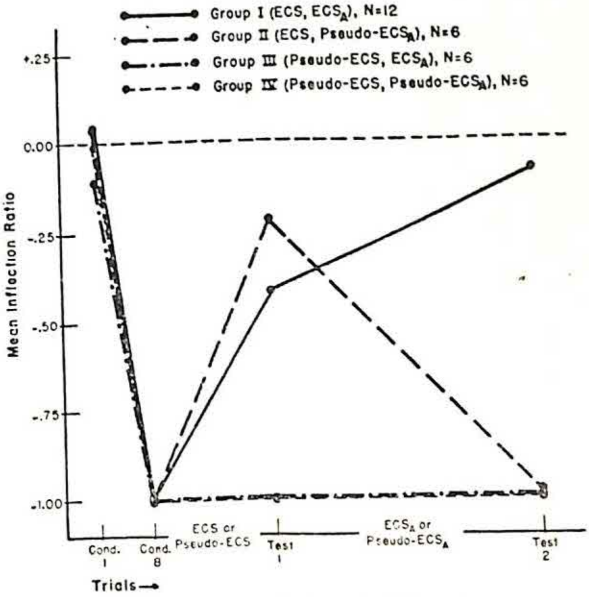

FIG. 1. The effect of additional ECS on the recovery of the CER after treatment

EXPERIMENT II

The Effect of "Additional" ECS on the Resistance of the CER to Delayed Treatment

Method

Subjects. Forty-one naive, male, albino rats, 60 to

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[1] All χ^2 values are corrected for discontinuity.

90 days old at the beginning of the experiment, served as *S*s.

Emotional conditioning procedure. The training in lever pressing, emotional conditioning, and testing for retention of the CER followed the same procedures as in Experiment I, except that the single retention test followed conditioning by a much longer interval, as indicated below.

Electroconvulsive shock. The apparatus and procedure were as described for Experiment I. The main, intensive series of 21 ECS, given 3 per day for 7 days, began either 32 or 62 days after the last conditioning trial. The 15 "additional" convulsions, ECS$_a$, were given 1 every other day over the 30 days immediately *preceding* the main series of 21 ECS. ECS$_a$ started either 2 or 32 days after the last conditioning trial.

Plan of the experiment. Here the main series of 21 ECS was postponed for a prolonged interval following conditioning of the CER. During this interval, some of the animals received ECS$_a$ to reveal whether the "additional" convulsions made the CER less resistant to attenuation by the delayed intensive treatment.

After the eighth emotional conditioning trial, the animals were divided into groups, roughly equated for the strength of the CER as it appeared to develop during the conditioning trials, and treated as follows:

Group I received ECS$_a$, ECS, and a retention test on the fourth day after the last ECS ($N = 18$).

Group II received pseudo-ECS$_a$, ECS, and a retention test as above ($N = 5$).

Group III received ECS$_a$, pseudo-ECS, and the test ($N = 5$).

Group IV (untreated controls) received pseudo-ECS$_a$, pseudo-ECS, and the retention test ($N = 5$).

Group V rested in the home cages for 32 days, then received ECS$_a$, ECS, and the retention test ($N = 5$).

Group VI rested for 32 days, then received pseudo-ECS$_a$, ECS, and the retention test ($N = 3$).

The first four groups provide the main data for the experiment; groups V and VI are supplementary in that they were included to find out whether a prolonged rest period in the home cages prior to ECS$_a$ would markedly alter the effects of the "additional" convulsions.

All animals were on 23-hr. water deprivation for the conditioning runs and retention test, with free access to food in the home cages. All animals had free access to water, as well, during the rest and treatment periods.

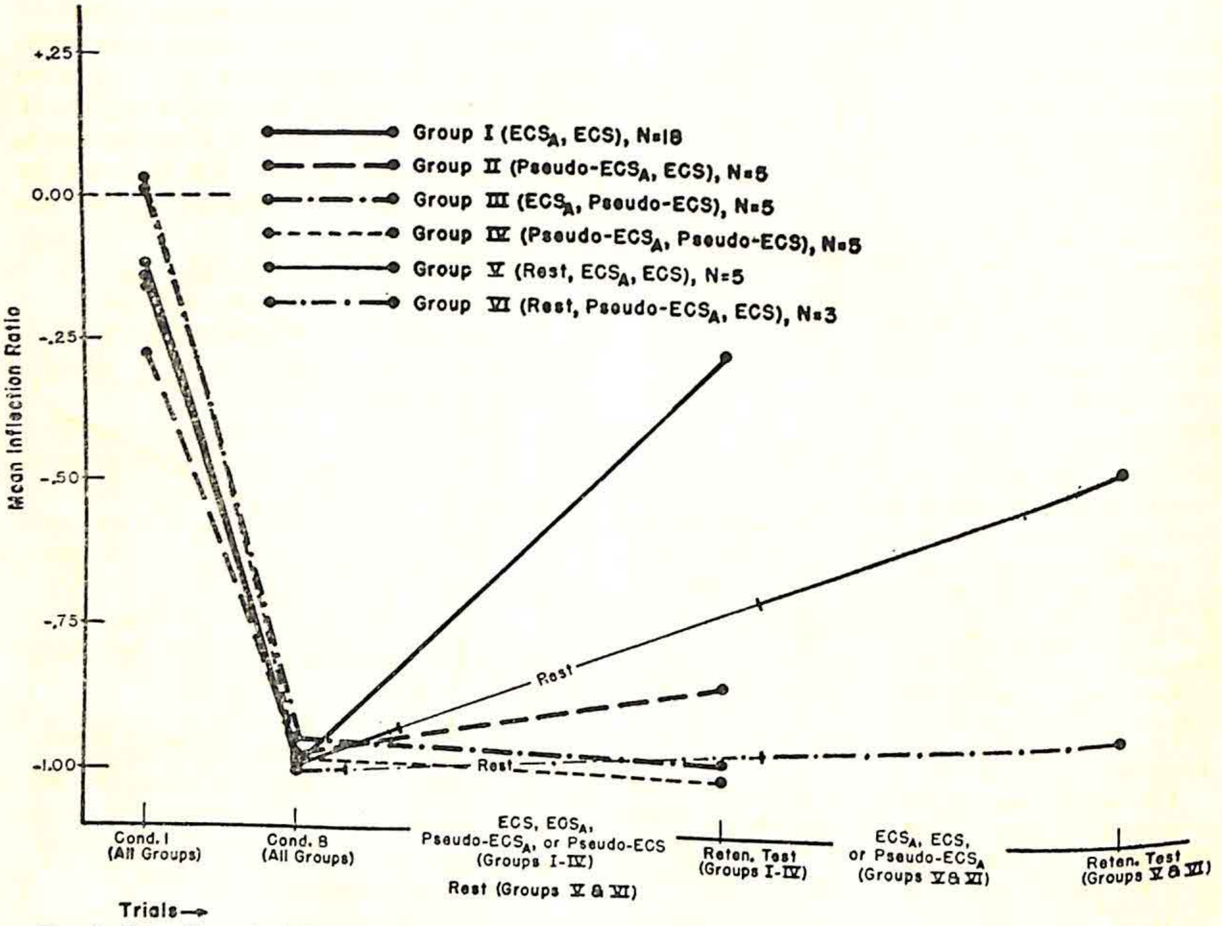

FIG. 2. The effect of additional ECS upon the resistance of the CER to attenuation by delayed treatment

Results

Figure 2 shows the mean inflection ratios for each group for conditioning trials 1 and 8 and for the retention test. The sharp negative shift in the ratios from trial 1 to trial 8 reflects the development of the CER. The attenuating effect of ECS_a added to ECS appears clearly as a substantial positive shift in the mean ratios between conditioning trial 8 and the retention test for group I. All animals in this group showed attenuation in the CER, with the smallest shift being from -1.00 to $-.66$ and the largest from -1.00 to $+.29$. Three of the animals receiving ECS only (group II) and one of the group III animals (ECS_a only) showed positive shifts, all of lesser magnitude. The difference between group I and group III in frequency of positive shifts is significant ($\chi^2 = 12.31$, $p < .01$), indicating that ECS plus ECS_a had more effect than ECS_a alone. Similarly, the significant difference between groups I and II in number of positive shifts indicates that ECS plus ECS_a had more effect than ECS alone ($\chi^2 = 3.65$, $p < .05$). In this last instance, the outcome of Experiment I provides the hypothesis that justifies the use of a "one-tailed" test of significance (7). And the difference in frequency of positive shifts in the inflection ratio between group I and groups II and III combined, from trial 8 to the test, is highly significant ($\chi^2 = 10.41$, $p < .01$).

The supplementary data provided by groups V and VI suggest quite strongly that a comparatively long rest period prior to ECS_a does not materially alter the effects of the "additional" convulsions.

As expected, the untreated control animals of group IV showed no attenuation in the CER from trial 8 to the test.

DISCUSSION

Both experiments yielded the expected results. "Additional" ECS (ECS_a) following the intensive series of convulsions prevented the recovery or reappearance of the CER in Experiment I. Similarly, animals given "additional" ECS prior to delayed intensive treatment clearly showed attenuation in the CER after the intensive series in Experiment II. Both ECS and ECS_a were required to produce these effects clearly; neither series of convulsions alone sufficed.

In Experiment I, the "additional" convulsions were spread out over most of the 35-day period between the intensive ECS and test 2, which tested for recovery of the CER. In this instance, ECS_a could have produced its effects in several ways, singly or in combination. The ECS_a could have prolonged or otherwise prevented the dissipation of those physiological consequences of the intensive ECS responsible for the initial attenuation of the CER on test 1. Or the ECS_a, thus dispersed, could have interfered with the increase in strength of the CER which usually develops with rest and/or elapsed time and which may be responsible for the normal post-ECS recovery of the CER. Or the CER may not have reappeared in those animals given both ECS and ECS_a simply because they received more convulsions.

The data from Experiment II, in which ECS_a made the CER less resistant to delayed intensive treatment, suggest strongly that the ECS_a did interfere with the increase in strength of the CER. The intensive ECS, starting 32 days after conditioning, presumably would not have been able to attenuate the CER if the response had increased in strength materially during the interval.

Beyond this point, however, the data are indecisive. Further experimentation will be required to show whether ECS_a, in Experiment I, also could have prolonged directly the effect of the intensive series of convulsions. Similarly, some possibility remains that the CER's in both experiments were attenuated more effectively by the combination of ECS and ECS_a largely because the animals received more convulsions. This seems somewhat unlikely, however. Convulsions given only on alternate days have comparatively little effect on CER's as strong as those used here. The ECS_a alone did not produce any significant attenuation in these experiments. Further, in another experiment, a series of 21 ECS, given 1 every other day, produced only the slightest attenuation in a CER based on six conditioning trials, as compared with the eight-trial CER used here (4).

The data from earlier research (1, 2) plus the data presented here suggest that the "additional" convulsions produced a somewhat more substantial effect on the CER than one would expect 15 convulsions, given 1 every other day, to have by virtue of their number alone. After all, the post-ECS recovery of the CER represents an overriding of the effect of 21 convulsions, given 3 per day for seven days. Similarly, the CER a month after conditioning effectively resists attenuation by 21 ECS given according to this same intensive schedule. Thus, pending completion of current research on the effect of massed and distributed ECS, it seems reasonable to suggest tentatively that the "additional" convulsions produced their effect in substantial part by interfering with the increase in strength of the CER which normally develops as a function of rest and/or elapsed time.

CONCLUSIONS

1. "Additional" convulsions, given after the intensive series of 21 ECS, prevented the post-ECS recovery of the CER.
2. "Additional" convulsions prior to delayed intensive ECS made the CER less resistant to attenuation by the delayed treatment.
3. The data suggest, tentatively, that the "additional" convulsions produced these effects in part by interfering with the increase in strength of the CER which normally occurs as a function of rest and/or elapsed time.

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EFFECTS OF ELECTROCONVULSIVE SHOCKS ON WILDNESS AND SAVAGENESS IN FERAL RATS[1]

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The purpose of this investigation was to survey the immediate and cumulative effects of electroconvulsive shocks (ECS) on wild and savage behavior of feral rats, trapped as adults and subjected to ECS without systematic taming.

Earlier experiments in this laboratory showed that certain types of innate behavior in albino rats, such as nesting by males and females (4, 5) and parental behavior in parturient females (3), are abruptly altered by a short course of ECS. These effects are more clear-cut and universal than any reported on learning or postconvulsion performance of maze and discrimination habits that have come to our attention.

Although frequent mention has been made of emotional disturbances in rats receiving ECS, the behavior cited is usually mild; ofttimes it could be classified more specifically as startle, body tenseness, irritability, pugnacity, or phobic avoidance of situations, without doing any injustice to the conventional meanings of these terms. Therefore, it may be possible to advance the frontier of knowledge on emotional behavior somewhat by making ECS in feral rats the object of study. In them the bodily expressions of timidity, wildness, and savageness are writ large if examined prior to systematic taming (5, 7).

SUBJECTS

In all, 60 rats were trapped in a granary near Palo Alto, California. When they entered the room at night to feed, they were shunted into a retaining cage without handling. This cage was transported to the psychology laboratory where each rat was caught by gloved hands and transferred to an escape-proof metal cage, 3 or 4 rats to the unit. Five of the 60 were judged to be less than two months old, as indicated by shape of snout and length of tail; the others represented all ages from early adult to middle age as judged by tail length, body conformation, and rigidity of the bones and cartilage of the chest. All became somewhat gaunt during the first week, probably because of inexperience with water bottles, an unfamiliar diet of Purina Dog Chow, and confinement with strange, bellicose rats in cages that afforded little opportunity for escape from aggressors. During the first week their cages were approached by us only as necessary to fill water bottles and supply food.

RESULTS

Opisthotonus in Convulsions

Motion pictures of convulsions in tame albino rats usually show, on release of the electrical discharge, a momentary stiffening of all limbs which "bounces" the animal slightly into the air. Then characteristically follows momentary limb flexion in which the four legs are "tucked" down against the abdomen, and the animal topples over on one side; the mandible is pressed against the neck; and the back is arched dorsally. Next, the limbs are gradually extended so as to present a "jackknife" posture. They may remain more or less rigid and perpendicular to the body axis for a few seconds or be extended backward gradually and stiffly until the forelegs lie against the abdomen and the hind legs extend rigidly to the rear of the body. During the backward extension of hind limbs there is vigorous contraction of dorsal muscles of the back which continues until a slight ventral bowing of the spine is apparent. This final posture, which sometimes appears in man during convulsions, is called opisthotonus.

During the preliminary study of ECS in feral rats, opisthotonus was rarely seen. In this respect their convulsions frequently differed from those of the albino rats. To quantify the difference, the following tests were made. Ten feral rats, five of each sex, were matched for weight and sex with similar numbers of albinos. Beginning on the sixth day after the feral rats were trapped (second time of handling), a course of ECS was begun in

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[1] This study was financed by a grant from the Scottish Rite Dementia Praecox Research Fund, New York City, to which grateful acknowledgement is made. I am indebted to Drs. Irwin N. Katz, Paul B. Porter, and Donald W. Taylor for technical assistance in several phases of the study.

which each feral rat received one convulsive shock on ten consecutive days. Convulsions were induced by a current of 45 ma., applied for .2 sec. through electrodes attached to the ears. The albinos were similarly treated. One trained observer, in addition to the author, who handled the animals, made notes on the physical patterns of convulsions. In a few instances motion pictures were made for supplemental study.

Of 100 convulsions in ten feral rats, only 38 per cent showed the characteristic opisthotonus as compared with 78 per cent for 100 convulsions in the ten albino rats. Seven of the ten feral rats (five males and two females) never assumed this posture, as compared with two of the domestic albinos (one of each sex). There was no clear-cut change in frequency of opisthotonus between the first and the last of the ten shocks in either group. Moreover, subsequent study of feral rats in other experiments has not indicated any change in the likelihood of its occurrence in the course of one daily shock for 20 days.

We do not have a satisfactory explanation for the difference between feral and domestic strains in frequency of opisthotonus. However, without suggesting essential similarity in causal factors, the study of Maier and Glaser (2) is worthy of recall here. They reported that a period of "dousing" with or struggling in cold tap water greatly reduced the probability of convulsions in rats that, soon afterward, were subjected to auditory stimulation. Also, Fuller and Rappaport (1) demonstrated that cold water (5° C) immersion of a strain of mice that was highly susceptible to lethal convulsions brought on by auditory stimulation gave almost complete immunity. By varying the experimental procedures they showed that lowered body temperature, quite probably, was a more important causal factor of this immunity than several other variables such as wet skin, exhaustion from struggling, unpleasant stimulation, and psychological agitation from handling. The foregoing and the present study have in common a high degree of activation of the somatic and also the autonomic nervous system just prior to application of convulsion-inducing stimuli. Whether it is this that provides the inhibiting effect for audiogenic seizures on the one hand and modification of the physical pattern of electrically induced convulsions on the other has not yet been ascertained.

Additional experiments with feral rats along lines similar to those of Fuller and Rappaport and also additional work with feral strains that have been reared from birth to maturity with sufficient taming to allay timidity, wildness, savageness, and struggling when under manual restraint would seem desirable. Quite logically such experiments should precede the more time-consuming attempts at genetic analyses in which evidence for a fundamental hereditary mechanism that could account for the obtained difference in opisthotonus is sought.

Resumption of Wild and Savage Behavior after ECS

Tests were made with ten feral rats to determine how soon the characteristic timid, wild, and savage behavior would reappear following an ECS. So ever-ready are feral rats to hide, to fend off a would-be captor, and to effect their escape by biting, scratching, and lurching that it is reasonable to assume that the postshock reappearance of these responses will reflect the temporal progress of redintegration of emotional syndromes, which momentarily are suppressed by ECS.

Ten wild rats weighing from 250 (f.) to 475 gm. (m.) were used. These had been in the laboratory for five days and handled only once prior to being caught for this study. One trained assistant, using a one- to three-point scale, rated the behavior of each rat on the items of Schedule A, called the "table situation." In all, four ratings were made: one just prior to ECS, and the other three at the end of the first, second, and fifth minute after ECS.

All the animals resumed breathing before the end of 1 min. postshock. When touched with a pencil at the end of minute 1, they usually scrambled to their feet, but did not hiss, bite, or struggle vigorously to escape when held by the tail. Most of them crouched and remained immobile on the table during the second minute, if not alerted by contact, a sound, or an object moving within the visual field.

When grasped firmly by the tail at the end of minute 2, however, all struggled, lay back

SCHEDULE A

Ratings for Timidity, Wildness, and Savageness; Scale, 0–3

I. Handling in home cage of hardware cloth (18 in. by 12 in. by 8 in.); 3 rats per cage
  a. ( ) running and milling to avoid being caught; biting others
  b. ( ) hissing; open jaws; threatening
  c. ( ) squealing; biting; struggling when grasped
  d. ( ) squirming; lurching in hand of E
  e. ( ) pulls away when held by tail; turns and bites
  f. ( ) ____________________

II. Manipulation on table top (3 ft. by 4 ft.); held in gloved hand
  a. ( ) jumps; lurches; squirms intermittently
  b. ( ) doubles up or turns to bite when stroked
  c. ( ) hisses; opens jaws; squeals when touched on nose
  d. ( ) snaps at finger held before mouth or nose
  e. ( ) pulls away when held only by root of tail
  f. ( ) ____________________

III. Large, wire-covered box (6 ft. by 3 ft. by 18 in.); small blanket and grain sack loosely lying in one corner
  a. ( ) lurches to escape hand when deposited on floor
  b. ( ) runs and dodges to avoid recapture
  c. ( ) squeals; hisses; opens jaws as hand approaches when cornered
  d. ( ) dashes to cover; goes beneath blanket
  e. ( ) remains hidden while experimenter is near
  f. ( ) ____________________

the ears, and bared the teeth; also, they usually bit the glove, squealed, or hissed; some urinated and defecated (see Fig. 1). When set down gently after the second minute's handling, all of them immediately ran if free to do so and would leap from the table if no manual restraint was imposed. If allowed their freedom, they leaped to the floor and then rapidly ran to a wall of the room, where they "froze" against the washboard or ran along it as if seeking cover or an opening. During the next 3 min. (third to fifth) considerable variation in the behavior of those that were released in the room was noted. Some ran if approached; some remained "frozen" against the wall; others reared on the hind legs in a posture denoting readiness for attack, with forefeet extended to ward off an approaching hand and with ears laid back and teeth bared. Sometimes there was hissing, squealing, biting, urination, and defecation if *E* pursued them into a corner or otherwise blocked the avenues of retreat.

During the next 10 min. (i.e., sixth to fifteenth, postshock) those that were given complete freedom in a large room (15 ft. by 15 ft.) gradually became indistinguishable from normal feral rats in responding to *E*'s movements or in the discovery of places of concealment in the room (such as a hole in the floor, a wall-type radiator, a burlap sack loosely arranged on the floor, or a cupboard moved slightly away from the wall).

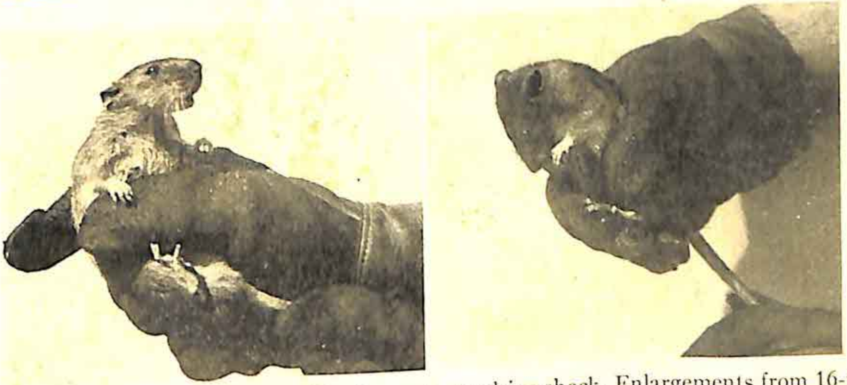

FIG. 1. Responses of feral rats at end of 2-min. postconvulsive shock. Enlargements from 16-mm. film.

The postshock observations of tame, albino rats under conditions essentially like those for the feral rats indicated that they did not display the same types of vigorous effort to fight or to escape from *E* during the first 2 min. as had the feral rats. There was no evidence whatever of postconvulsive timidity, wildness, or savageness. From the sixth to the fifteenth minute they moved about the room slowly as if to explore novel objects rather than to escape a would-be captor.

The foregoing experiments indicate roughly the speed of recovery of innate responses which we presume to be organized (though not wholly directed) by the archipallium and hypothalamus, as opposed to learned responses which, we presume, are organized and directed primarily by neocortical centers. Possibly a somewhat similar approach with recently caught feral rats and thoroughly tamed wild strains that have acquired maze or discrimination habits might yield illuminating comparative data on speed of recovery of responses that are cortically, as opposed to hypothalamically, organized.

Cumulative Effects of ECS

An attempt to appraise the cumulative effects of repeated convulsive shocks was made with 16 feral rats, half of which received daily shocks for 25 consecutive days while the others received pseudoshock and a similar type of handling. Each of these rats was removed from its cage on the fifth day after arrival in the laboratory to make a 3-min. motion picture that would provide a sample of the wild and savage behavior of each animal. No further handling occurred until the eighth day after trapping, when the first phase of this study began.

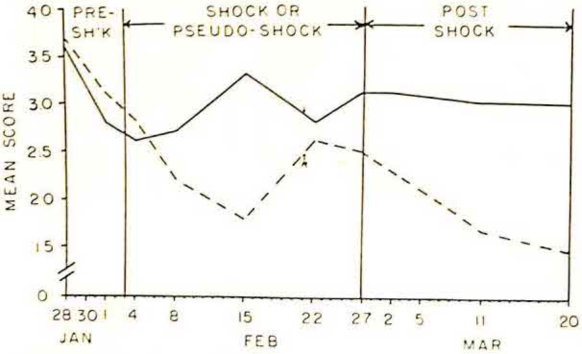

FIG. 2. Ratings of 8 feral rats undergoing course of ECS and 8 feral controls undergoing pseudoshock and similar handling. The calendar dates of ratings are shown on the abscissa. On Feb. 21 (indicated by letter *R*) all animals of both groups were released in a large room for 4 hr.

Two graduate students assisted the author. Previously they had practiced rating the behavior of feral animals that were being put through the routine called for in Schedule A (*vide supra*). When possible, values ranging from 0 to 3 are assigned to the items of this schedule. The 0 denotes tameness of the grade displayed by much-handled albino rats, and 3 the vigorous struggling to escape, vicious pugnacity, or cowering and concealment efforts shown by feral rats. The two observers in this study agreed closely on values assigned to what they could observe equally well, but because of the unpredictability of a wild rat's movements the two were not always watching the same details. For this reason incomplete records on the part of both observers were the rule. However, it became apparent that our needs could be served adequately by having each observer make a "global" appraisal of the rating sheet for each animal, giving it a value ranging from 0 to 5. The 0 described the records of a tame, albino rat, and the 5 that of the wildest, fiercest feral animal in the group.

Group means[2] based on the average of these "global" ratings provide the data for Figure 2. There was a small drop in the mean of ratings of both groups in the preshock period. This decline continued in the nonshock group, but not in the convulsed group. On the eighteenth day of the study (Feb. 21, on the abscissa calendar) an innovation was introduced. Both groups were released in a large, poorly lighted attic room with floor space of about 300 sq. ft. They were free to seek shadows and crannies for concealment, or sills and girders over which to climb from floor to roof. They were left in this room undisturbed for a 4-hr. period. Then all were caught manually and returned to their proper cages. Catching the animals involved a considerable amount of commotion because most of them had to be pursued, cornered, and seized, or pulled from a hiding place. During recapture no readily observed difference was noted between nonshocked and shocked animals. This finding was not altogether surprising, for previous studies had shown that initial taming effects in feral rats are "situational" only, and that, when given their freedom for a short time, they quickly revert to type (5). This accounts for the rise in mean value for the controls for a few rating periods following the large-room experience.

The mean of the convulsed group ceased to decline soon after the inauguration of ECS, and thereafter fluctuated only within narrow limits during the following days of the study. Release of these animals in the large room produced little effect on their mean scores.

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[2] Because of the small number of cases involved in this part of the study it seems appropriate to emphasize only the trend of results; moreover, individual differences in each group are relatively great. For the period of shock and for postshock the t is significant at the .05 level; for the individual days of Feb. 15, 22, 27 and Mar. 5 and 20, the t is significant at the .05 level only on Feb. 27 and Mar. 20.

Furthermore, to our surprise, there was no decline in the mean scores of the convulsed group during the postconvulsive period.

Several speculations might be advanced to account for the absence of "pseudotaming" in the shock group: (*a*) It might be attributable to increased tension and irritability caused by ECS, akin to what is sometimes seen in milder form in convulsed, albino rats and evidenced by tensing of the body when they are grasped or by the fighting of cagemates; if so, the behavior was more general and more extreme in feral rats than that ever reported for tame rats. (*b*) It might also denote that the convulsive animals have an intensified aversion to being handled; they may experience some pain and discomfort (which are normal aftermaths of convulsive shocks in man) in the manipulations required by Schedule A. (*c*) Again, speculating with even less basis in fact, one might regard it as the analogue of stereotyped, unadaptive behavior sometimes appearing in ill-defined learning or retention situations; in this situation absence of "pseudotaming" would be the analogue of persistent, stereotyped errors or "position" habits in something like a two-stimulus discrimination box. In the light of present knowledge all the foregoing suggestions are highly speculative, the last being even less plausible than the others.

As a further step, a repetition of this latter phase of the study is needed to test the validity of the present findings that "pseudotaming" does not proceed as in normal feral rats. The evidence at hand is clear-cut, however, in respect to failure to show sudden, spectacular elimination of wild and savage behavior as a result of daily ECS; certainly there is nothing like the abrupt reduction or elimination of nesting behavior of the domestic male or female rat following a course of ECS.

SUMMARY

An exploratory study of the effects of ECS on timidity, wildness, and savageness in feral rats was made by comparing these effects, when possible, with the characteristic effects of ECS in tame, albino rats. The most noteworthy findings are as follows:

1. Significantly fewer of the feral than of the tame albino rats display in grand mal convulsions the rigid backward extension of the hind legs and bowing of the spinal column. No satisfactory explanation of the differences in frequency of this type of opisthotonus has been formulated.

2. All observed types of activity denoting timidity, wildness, and savageness in feral rats begin to manifest themselves unmistakably again between 1 and 2 min. post-ECS. Within 15 min. the behavior is so nearly like that of their preshock period that simple laboratory tests fail to bring out differences.

3. A course of ECS, once daily for 20 days, did not greatly alter the individual patterns of "emotional" responses in the feral rats. Unlike control feral rats, similarly handled with pseudoshock, there was no clear-cut suppression of wild, savage behavior, thereby producing a kind of "pseudotameness" seen in their controls. Further work on this point is warranted to establish the validity of the obtained differences.

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CONDITIONED AND UNCONDITIONED EMOTIONAL DEFECATION IN THE RAT[1]

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Bindra and Thompson have reported negligible correlations between "emotional defecation and urination" and two other behavioral indicators of general emotional disturbance in the rat, "timidity" and "fearfulness" (1). They concluded that "emotional elimination is not a generally valid instrument for measuring fearfulness." They went on to point out, quite legitimately, that "emotional" and "nonemotional" strains of rats, selectively bred on the basis of elimination as an index of emotionality, actually may be "high elimination" and "low elimination" strains. These, they argued, may differ mainly with regard to "autonomic reactivity" or "susceptibility to a very general type of emotional disturbance, which leads to defecation and urination, under conditions of any unusual stimulation." While Bindra and Thompson do not object to "emotionality" as a neutral but inclusive term to describe this particular susceptibility, they state that such emotionality "is not to be equated with fearfulness or timidity and that it may have little to do with what is normally called emotion or emotional behavior" (1, p. 45).

The present paper does not intend to argue about the existence of a trait "emotionality" in the rat or the existence of an "emotional" or "fearful" type among rats. Nor does it intend to argue that "emotional elimination," as presently measured, necessarily is either a suitable measure of this hypothetical trait or an indicator of this hypothetical type. The history of type and trait psychologies, as they have developed in connection with personality theories and the study of individual differences, reveals the ease with which such discussions collapse into arguments about definition.

Rather, this paper intends primarily to show how defecation is related to emotion and emotional behavior by demonstrating the relationship between the incidence of defecation and the acquisition and loss of a conditioned emotional response of the "fear" or "anxiety" type—the CER (see 2, 6). The data for this demonstration were generated by experiments originally performed for a somewhat different purpose. They apply here, however, because they not only bring out the relationship between defecation, painful stimulation with electric shock, and "emotional conditioning," but also because they typify the events which consistently have inspired our confidence in this humble indicator of emotional disturbance in the rat.

EXPERIMENT I

Defecation as a Component of a Conditioned Emotional Response

Method

Twenty-four naive, male, Sprague-Dawley albino rats, 60 to 90 days old at the beginning of the experiment, served as *S*s for the emotional conditioning. Eight of these animals served as *S*s for the experimental extinction by nonreinforcement of the CS. The remainder received ECS after conditioning, as part of their service in the original experiment (see 7), so their performance during extinction is not relevant here.

The conditioning of these animals is described in the paper covering the original experiment. In brief, all 24 animals received a total of eight emotional conditioning trials, one per day for eight consecutive days, in the "grill box," a chamber with a grill floor and a transparent wall to permit observation of the animal. Each trial consisted of a 3-min. presentation of a strong intermittent light as the CS (150-w. bulb 3 ft. above the grill floor) terminated contiguously with two momentary painful shocks to the feet (approximately 1.5 ma.), as the UCS, delivered through the floor. During conditioning and extinction, the CS was introduced around the beginning of the fifth minute of the standard 12-min. runs.

Beginning on the tenth day after the last conditioning trial, eight animals received a total of four extinction trials. Four of these animals rested for 29 days between the first and second extinction trials; the others received four extinction trials, one on each of four consecutive days starting on the tenth day.

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The latter group then had six more extinction trials, rested, and then received a "spontaneous recovery" test when the first group received its second extinction trial. The extinction data for both of these groups for the four trials are combined because the 29-day rest for the one group had no discernible, differential effect upon any aspect of performance to be discussed here.

All animals were on a 23-hr. water-deprivation schedule, with free access to food in the home cages, during conditioning and extinction. All had free access to water, as well, during the rest periods.

In this situation, the CER typically appears as a clear-cut "freezing" or crouching reaction upon presentation of the CS. The apparatus permitted observation of both the moment at which the animals defecated and the relation between this response, presentation of the CS and UCS, and the crouching as a postural expression of the CER.

Results

The typical CER developed during conditioning. Interestingly enough, the CS elicited only exploratory behavior the first time it was presented—no crouching or defecating—even though the light was bright and glaring enough to be an aversive or disturbing stimulus in its own right. All animals showed the CER by the fourth conditioning trial or before; all that were to be extinguished showed the CER on the first extinction trial. On the fourth extinction trial, five of the eight still showed weak and sporadic CER's, indicating that the crouching response had not been eliminated yet by nonreinforcement.

The incidence of defecation (the number of different animals defecating) during each conditioning trial considered as a whole increased from 8 to 24 from the first trial, C 1, to C 8. For the eight animals subjected to extinction, the incidence of defecation dropped from 8 to zero from the first extinction trial, E 1, to E 4. Both trends are significant ($p < .02$).[2] Figure 1 shows the approximate point in each trial at which defecation occurred. Each curve in the figure indicates the incidence of defecation during each segment of each trial—the number defecating prior to presentation of the CS, during the CS, and following the CS and UCS during conditioning or the CS only during extinction.

The incidence of defecation following the UCS increased significantly between C 1 and C 2 ($p < .01$); defecation during the CS first increased significantly between C 2 and C 3 ($p < .01$). During trial C 2, the UCS elicited significantly more defecation than either the CS or placement in the apparatus (both $p < .01$). Defecation during the CS increased from C 2 to C 8, while, over the same interval, defecation following the UCS decreased significantly to return to its original C 1 level (both $p < .01$). And during C 8, the CS elicited more defecation than the UCS ($p < .01$). Similarly, the incidence of defecation was greater during the CS than during the other segments of the first two extinction trials ($p < .05$). Clearly, then, the CS acquired the power to "elicit" defecation and retained this control over the response through one extinction trial for all animals and over 29 days of inactivity, as well, for four of them.

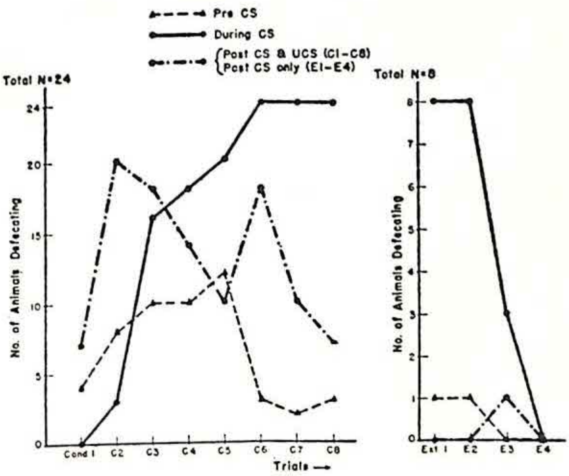

FIG. 1. The incidence of defecation during each segment of each conditioning and extinction trial

The joint occurrence of defecation and crouching or "freezing," as a general postural expression of the CER, substantiates the emotional and the conditioned nature of the defecation. On the twenty-ninth day after the first extinction trial, four animals received their second extinction trial; the other four animals, in the extinction group, received a spontaneous recovery test at the same time. A comparison between these two groups, for the first group following one extinction trial and for the second following ten, indicates nicely how the CER and defecation tend to covary. On this test day, five animals both defecated and showed the CER while three showed neither response. The relationship between crouching and defecation was significant ($p < .05$). Defecation not only appeared in conjunction with the CER in all the animals that had received only one prior extinction trial, but even reappeared after ten extinction trials in the one animal that showed spontaneous recovery of the CER.

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[2] All p values are for a two-tailed test of significance based on χ^2 corrected for discontinuity (8).

A question remains. Does defecation, as a response, have a sufficiently short latency and sufficiently regular duration to justify assigning it to a particular stimulus as in Figure 1? An unpublished experiment[3] provides pertinent data based on the performance of 20 female and 10 male albino rats, with 10 females on free food and water and the rest on the standard water-deprivation, free-food schedule. All received one 10-min. run in the grill box, with a burst of five momentary 1.5-ma. shocks introduced at the beginning of the fifth minute. Twenty-two rats defecated, in all cases starting within 10 to 90 sec. after the shocks, usually within 20 to 60 sec. All but two stopped defecating within 135 sec. after the shocks; the two exceptions stopped within 215 sec. These data strongly suggest that defecation starts and stops soon enough and regularly enough after disturbing stimulation to justify our description of it in Figure 1.

EXPERIMENT II

The Relationship between Emotional Defecation and "Timidity"

If defecation covaries so clearly with both conditioned and unconditioned emotional disturbances, one would certainly expect it to be correlated natively with other indicators of emotionality. To check on this expectation, Experiment II inquires into the relationship between defecation in a modified open-field situation (after Hall) and performance on a "timidity" or "shyness" test similar to that used by Bindra and Thompson (1).

Method

Sixty-two naive, male, Sprague-Dawley albino rats, 70 to 80 days old, served as *S*s. These animals received no preliminary handling prior to the tests. All animals received the open-field test first and the "timidity" test second, 10 days later.

The *open-field test* employed a wire mesh field, octagonal in shape, with 12-in. walls of battleship gray. The field was approximately 4 ft. in diameter, well illuminated, and elevated 33 in. above the floor. Each animal received four individual 4-min. runs, one on each of four consecutive days. All animals had free access to food, but no water was available in the home cages except during a 2-hr. period which terminated 1 hr. before each test. A record was kept to indicate which animals defecated or urinated, and how many times, during each minute of each test run.

The *"timidity" test* consisted essentially of a determination of the amount of time it took the hungry rat to emerge from the living cage onto a 5-in. by 30-in. runway placed in front of it to seize one of three pellets of food placed 12, 21, and 30 in. away from the cage. The scores consisted of time to actual taking of any one of these pellets, as well as both time to placing the forepaws and time to placing all four feet on the runway. The animals were placed in individual living cages three days before the test; all had free access to water but were on a 23-hr. food-deprivation schedule during this time. On the fourth, or test day, at the usual feeding time, the living cage was placed at the end of the runway for 15 min. Then the cage door was opened and the animal given a maximum of 30 min. to emerge and take a pellet.

Results

The results agree with those reported by Bindra and Thompson (1). The data revealed no appreciable or statistically significant relationship between defecation during any one run or all runs in the open field and "timidity," regardless of the methods employed for scoring either test. Though both tests distributed the animals over a range of scores and isolated extreme cases, neither rank-order nor contingency methods revealed any systematic covariation between the tests. Nor did the extreme scores on one test appear to be associated in any systematic manner with scores on the other.

DISCUSSION

Experiment I reveals a close functional relationship between defecation and emotional disturbance in the rat. In fact, for these data defecation almost could have substituted for crouching or "freezing" as the conditioned emotional response. Defecation would appear to have a good deal to do with what is normally called emotion or emotional behavior in the rat! But Experiment II, in agreement with results reported by Bindra and Thompson, reveals no correlation between defecation in the open field and performance on the "timidity" test. In Experiment II, an animal predisposed to emotional upset (i.e., "emotional") should have been disturbed to some degree by both test situations—by their novelty only, if for no other reason. If performance on the "timidity" test does, in fact, reflect some aspect of emotional disturbance and if defecation, as such, is a reliable indicator of a generalized emotional response, Experiments I and II would appear contradictory.

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[3] We are indebted to Mr. William Beckwith for his help with this experiment.

Under what conditions, then, does defecation reflect emotional disturbances? Our data suggest that it does so reliably only when the emotional disturbance is fairly strong; defecation, as a component of the general reaction to emotional disturbance, appears to have a comparatively high threshold. For example, the light serving as the CS in Experiment I was bright and glaring enough to have some unpleasant and disturbing properties of its own. Incidental observations on the effect of this stimulus have revealed that albino rats move away from it in the standard double-grill avoidance apparatus, if given the chance. Yet this CS elicited no defecation in trial C 1 (see Fig. 1) prior to the first reinforcement with shocks.

Further, as the intensity or amplitude of the CER decreases as a function of nonreinforcement during extinction, defecation disappears sooner than the crouching or "freezing" response. By trial E 4, in Experiment I, the incidence of defecation had dropped to zero while 5 of the 8 animals still showed weak CER's. Data on the extinction of the CER established in the Skinner box, where the CER is superimposed upon a lever-pressing habit, typically show a similar trend. Here a strong CER appears as a cessation in lever pressing during presentation of the CS (see 6, 7). In one experiment, 11 rats received one extinction trial per day for ten days, after the CER had been established by eight conditioning trials. All animals both defecated and showed the CER on the first extinction trial. On the tenth, only 3 animals defecated while 10 still showed a complete cessation of lever pressing during the CS—a significant difference ($p < .05$).

From these observations, defecation in the open field would seem a relatively insensitive test for predisposition to emotional disturbance. Not only does emotional defecation have a high threshold, but the test situation itself is bland compared with stimuli such as electric shocks. Very likely, the open field did not disturb the homogeneous and rather phlegmatic Sprague-Dawley *S*s either very intensely or to markedly differing degrees. A substantial portion of the defecation here probably was a function of factors other than emotional disturbance. The adaptation indicated by the significant decrease in incidence of defecation from the first to the fourth run in the open field ($p < .01$) suggests that emotional disturbance or something like it could have made some contribution to the scores (3). But the tetrachoric correlations between runs 1 and 2 and between 1 and 4 of +.55 and +.62, respectively, indicate a relatively low order of test-retest reliability for the open field in this experiment.

Considering all this, the lack of correlation between the open-field and "timidity" tests in Experiment II is hardly surprising, particularly since the "timidity" test probably is neither perfectly reliable nor perfectly valid as an indicator of emotional disturbance or "disturbability." Bindra and Thompson used both male and female and hooded as well as albino rats—a somewhat more heterogeneous population than served in Experiment II. But a *considerably* more heterogeneous population with regard to threshold for emotional disturbance might be required to produce the kind of validating data previously reported for the open-field test (for general overviews see 4; 5; and 9, pp. 98–100). Probably the variance in defecation in the open field becomes primarily a function of emotional disturbance only when the test really disturbs a substantial proportion of the *S*s.

CONCLUSIONS

1. Defecation can serve to indicate conditioned emotional disturbance of the 'fear" or "anxiety" type. In fact, as a result of the conditioning procedure the CS actually acquired the power to "elicit" defecation as one component of the general emotional response. Defecation appears to have a somewhat higher threshold than the crouching or "freezing" component of the CER, however.

2. Defecation in the open field showed no

correlation with performance on a "timidity" test, in agreement with the findings of Bindra and Thompson. The placidity and homogeneity of the *S*s, together with the probable insensitivity of defecation in the open field as a test, could have produced these negative results.

3. While defecation is clearly related to what it seems proper to call emotion or emotional behavior in the rat, the relationship probably becomes unambiguous and reliable only when the emotional disturbance is substantial and reasonably intense.

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A SPATIAL GRADIENT OF ALTERNATION TENDENCY

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The inhibitory effect that follows a response has some well-known properties. Among them are these: (*a*) it builds up when responses are made in rapid succession; (*b*) it dissipates spontaneously during a rest period, but not completely; (*c*) effortful responses tend to produce more of it; and (*d*) the effect spreads or generalizes to responses similar to the one producing the inhibition. Hull (1) has worked out the relationships of this response-produced inhibitory effect to a variety of behavioral phenomena such as extinction, spontaneous recovery, reminiscence, and the efficiency of spaced practice. One of the gaps in our knowledge about this kind of inhibition consists of the fact that no uniform gradients of generalization of response-produced inhibition have been reported in the literature. We have chosen to investigate this problem by a method recommended primarily by its experimental simplicity.

It has been demonstrated that a rat forced to make a left turn on an inverted L-shaped runway will then tend to alternate its response by turning right if soon after it is given a choice on a T-shaped maze (6). If we assume for the moment that this alternation tendency is produced by what we have been calling response-produced inhibition, it should be simple to test for a spatial generalization gradient of inhibition by forcing rats to make a left turn on an inverted L-shaped runway and then observing their frequency of choices for each path of a fan-shaped maze. A gradient would be obtained if the frequency of choice were greater for paths farther away (to the right) from the forced path.

The validity of our assumption relating alternation tendency and response-produced inhibition will be considered in a later section. If this assumption ultimately proves untenable, the present study may be viewed simply as a demonstration of an interesting behavioral regularity to be accounted for, along with other alternation phenomena, by some theory.

METHOD

Apparatus

A diagram of the fan-shaped choice point comprising our main piece of apparatus is shown in Figure 1. It is an elevated maze made up of five separate wooden blocks each approximately 36 in. long, 1½ in. wide, and 12 in. high. The maze was placed on the floor of a well-lighted room, providing a heterogeneous external stimulus surround. Portions of the maze could be removed manually to form the various runway combinations shown in Figure 1.

Subjects

The *S*s were 27 naive, female, albino rats from the University of Connecticut colony of Wistar-strain rats. Their ages ranged between 200 and 300 days with a mean of 260 days.

Procedure

Essentials. The basic elements of the procedure consist of two steps: the rats are first forced left or right on paths *A* or *D*, and then are given their choice of paths *A*, *B*, *C*, or *D* on the fan-shaped maze. If the rats choose a path whose direction is away from the forced path, they are said to alternate. Strength of alternation is measured by the frequency of alternation; direction of alternation is measured by the angular separation of the chosen path from the forced path.

Controls. Since it is our purpose to attribute alternation tendency to an inhibitory state produced by the response on forced trials, it is necessary to arrange some experimental controls for other factors capable of producing an alternation tendency independent of forced responses. Learned or unlearned preferences for paths other than the forced path are factors most likely to cause alternation. To minimize such preferences (or aversions) for different paths, the rats were given a long training period during which they were to acquire strong, presumably equal, habits of running to each of the four path positions. Equality was not always the result, so the extent of inequalities in path preference was assessed by giving the rats free choices on the fan-shaped maze before the forced trials were administered. Then an alternation measure was adopted which would partial out of the final result alternation due to these known unequal path preferences.

These control procedures are also effective in eliminating explanations of the results in terms of conditioned inhibition (6), but they do not preclude explanations in terms of exploratory tendency, a matter to be discussed presently.

Training. For each rat a daily training session included 10 massed runs to one of the four path positions shown in Figure 1. The intertrial interval was 10 sec.; the reinforcement, a 5-sec. feeding of wet Purina mash. The path receiving the practice was changed every day in a nonsystematic fashion. After 80 trials, the median running time of the group had been reduced to 2 sec., a final level maintained for 40 more trials.

All sessions in the entire experiment were run with the rats approximately 22 hr. hungry. All responses were reinforced with food. A 30-min. feeding of wet mash followed every session by an irregular period averaging ½ hr.

Alternation tests. Following the 12 daily training periods the rats were given 24 daily sessions of alternation tests. Each session included first a free choice on the fan-shaped maze to establish each rat's daily preference. Secondly, after at least a 30-min. interval, every rat was given a series of forced trials to either path *A* or *D*. The number of forced trials was either two or ten, with 10 sec. between trials. Thirty seconds later the rat was given a choice of paths on the fully reassembled fan maze as a test for alternation. This ended the daily testing period. From day to day the number of forced trials (either two or ten) and the direction of forced trials (either *A* or *D*) were changed in a nonsystematic manner for each rat.

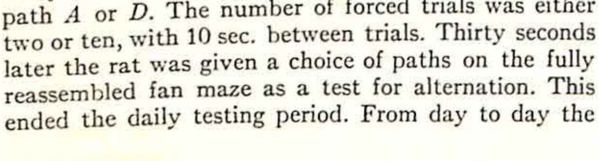

FIG. 1. Diagrams of the arrangements of the path units during training, forced trials, and test trials. The angle separating each of the goal arms *A*, *B*, *C*, and *D* from the next is 60°. *S* marks the starting point.

Measures. The number of times a rat chose a particular path in a series of 12 test trials constituted a measure of preference for that path. Such a measure could be obtained for each path from the series of 12 test trials given each rat *before* the forced trials and another from the series given after the forced trials. The difference between these two frequencies was a measure of the change in preference produced by the forced trials. Since the pre-forced-trials test frequency was subtracted from the post-forced-trials test frequency, a rat could obtain a "change" score ranging from +12 to −12 for each path. A positive score meant that a path was preferred more after forced trials than before; a negative score indicated the opposite. A zero score meant that the forced trials had no effect on path choice.

The specification of path was in terms of the angle separating the forced path from the chosen path. For example, a choice of path *C* on a day when forced trials were to path *A* was tallied as a 120° response. So, also, was a choice of path *B* when forced trials were to *D*.

Using these measures and specifications, it was possible to derive, for each path angle, two distributions of preference-change scores, one for the test series employing two forced trials, and one for the test series with ten forced trials.

It was possible also to obtain distributions of preference-change scores for test series of "zero" forced trials simply by comparing one day's pre-forced-trials test frequency with the next day's pre-forced-trials test frequency. Since it is known that the I_R effects of a series of ten forced trials do not last for 24 hr. (6), the daily changes in path preference measured by the pre-forced-trials tests provide us with an empirical base line of chance preference-change scores. In detail, the method of obtaining these scores differed from that of the previous preference-change scores in only one respect. Instead of subtracting the pre-forced-trials test frequency from the post-forced-trials test frequency, we subtracted the odd day's pre-forced-trials frequency from the even day's pre-forced-trials test frequency. Since there were 12 odd and 12 even testing days, a rat could get a preference-change score ranging from +12 to −12 for each path. This yielded one distribution of 27 change scores for each path angle, interpretable as the preference change produced by "zero" forced trials. Here, negative scores mean that a path was preferred more on odd days than even days. Positive scores have the opposite meaning.

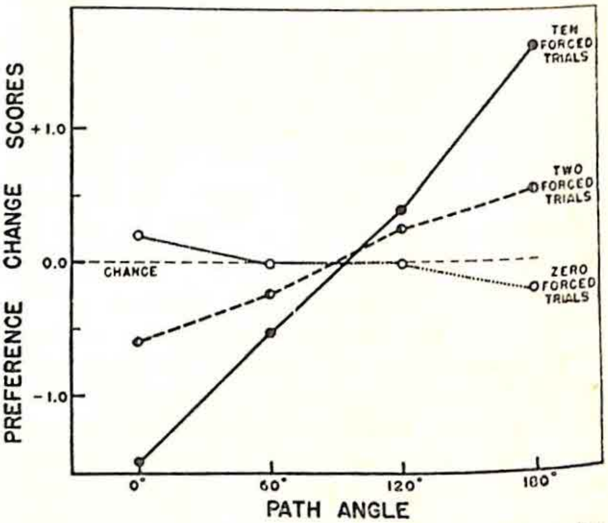

FIG. 2. The temporary changes in preference for different path angles produced by zero, two, and ten forced trials to the 0° path

RESULTS

The spatial gradients of alternation after zero, two, and ten forced trials are presented in Figure 2. The angle to which the rat is forced becomes his least preferred of the four paths. His preference increases uniformly for the paths farther away from the forced path. The effect of increasing the number of forced trials is to increase the slope of the gradient.

The absolute magnitude of the gradient is not small despite the fact that the possible score range is −12 to +12. The experimental design renders extreme scores unlikely. As an illustration, consider a rat having equal preference for the four paths before forced trials. Its 12 test responses before forced trials would be distributed 3, 3, 3, 3 over the four path angles. If this rat were a strong alternator it might, after forced trials, distribute its 12 test responses 0, 2, 4, and 6 over the four path angles (0°, 60°, 120°, and 180°, respectively). The alternation gradient of this strongly alternating rat as measured by preference-change scores would be −3, −1, +1, +3 over the four path angles, in order. The mean gradient after ten forced trials for the 27 animals plotted in Figure 2 is about one-half as steep as the gradient of this hypothetical rat.

Although the effects of path angle and number of forced trials on mean preference scores appear by inspection to be quite clear, it is possible that such mean differences may have occurred through errors of random sampling from a single common population of preference scores. To test this possibility, an analysis of variance technique was used on the scores comprising each gradient. Total variance was partitioned into a path-angle variance, an animal variance, and a residual-interaction variance (path angle × animal), the latter used as error term. The obtained *F*'s indicated that the zero-forced-trials gradient could easily have been produced by sampling error, but that the ten-forced-trials gradient would have occurred by chance less than once in a hundred times. The scores in the two-forced-trials gradient yielded an *F* not high enough to be significant at the .05 level of confidence. However, the fact that the shape, slope, and location of the two-forced-trials gradient are all about what would be expected makes us unwilling to conclude that this is a chance function.

DISCUSSION

Empirically, this experiment was successful in demonstrating with rats the orderly spread of a temporary response-produced disturbance of preferences among four paths. Theoretically, the phenomenon might be interpreted as the generalization of either a transient inhibitory state produced by responding, or an excitatory state generated by not responding. The choice would depend upon what one believed to be the cause of alternation. Hull's construct of reactive inhibition (I_R) has been used to give an account of other alternation effects (5, 6) and could be extended to apply here. On the other hand, the possibilities of an excitatory state built up by not responding have been pointed out by Montgomery (2). He believes that the rat alternates its choices on a simple T maze in order to explore the relatively fresh or novel stimuli of a just-previously-not-responded-to maze arm.

These two views have some differential consequences, a few of which have been put to experimental test. The results have unfortunately not been entirely in favor of only one of these explanations. For example, rats have shown a preference for alternation of an "approach" response (place alternation) rather than alternation of a "turning" response (response alternation), and this fits Montgomery's exploratory hypothesis very well (2). Not so favorable to Montgomery's view is Solomon's finding that an increase in response work increases alternation (4). This effect would be predicted by I_R theory. To add to a confusing picture, some evidence has been uncovered of both place alternation and response alternation in the same situation (3). Although the present weight of evidence indicates that alternation could be the result of the operation of either I_R or exploratory drive—or both,[1] our current preference for the I_R explanation is based upon the wide applicability of the I_R construct to a variety of similar phenomena and upon the inclusion of I_R principles within an existing general behavior theory. As a brief summary of what I_R theory will do in the domain of alternation effects, we offer the following list. Reactive inhibition principles will predict (*a*) the simple occurrence of alternation, (*b*) the increase in alternation with the number of forced trials, (*c*) the spontaneous dissipation in time of the alternation tendency, (*d*) the increase in alternation with increase in work, and (*e*) the occurrence of generalization of alternation. It may be possible to account for some of the place alternation findings without disturbing these theoretical accomplishments by using I_R theory in conjunction with a molar (approach-this-place) definition of response rather than the usual more molecular (turn-in-this-direction) specification of response.

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[1] Rothkopf and Zeaman (3) have offered a composite of these two types of explanations as an adequate but perhaps unparsimonious resolution.

Both theories must be further developed to account precisely for our obtained gradients. In one case there is needed a principle saying that the stimulus aspect of novelty generalizes along a spatial gradient; in the other we need merely to add to Hull's I_R Postulate 8 a section describing quantitatively how I_R generalizes. Both principles have additional behavioral consequences yet to be worked out. It is recognized that, as applied to the present situation, only one of the principles may eventually stand the test of deductive elaboration and further empirical checks. But in the meantime we may safely conclude that whatever theoretical factor is producing alternation must be such as to produce also a spatial gradient of alternation.

SUMMARY

Uniform spatial gradients of alternation tendency have been obtained by running rats down one path of a four-goal arm, fan-shaped maze, and then giving them a free choice of the four pathways. Other relevant factors being equal, the rats showed increasing preference for the paths farther away from the single path they had just been run on.

Forcing the rat to choose one path ten times in rapid succession causes its preference for the more distant paths to rise more steeply than the use of only two forced trials.

The spatial gradients of alternation were related theoretically to the generalization of reactive inhibition (I_R). The results were also seen to be consistent with the view that the rats were exploring a gradient of novel stimuli.

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THE AGE FACTOR IN MULTIPLE-DISCRIMINATION LEARNING BY WHITE RATS

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The early studies of Watson (11), Hubbert (4), and Liu (5) found that maze-learning ability increased up to 75 days, and that young rats were superior to older ones (up to 300 days). The work of Stone (8, 9) and Tryon (10) supports the view that learning ability reaches a maximum before 75 days and that no decline is evident during the first two years of life. However, Maier (6) found a difference in ability to perform reasoning tests in favor of 120- to 300-day-old rats vs. 50- to 90-day-old rats. Munn summarizes the literature on age with this comment: "Learning ability appears to increase with age up to about thirty days and then to remain fairly constant until the rat is about two years old, an age comparable with sixty years in man" (7, p. 358).

With apparatus and techniques recently developed (1, 2, 3) it was decided to explore this problem again before investigating the effects of potentially harmful stimuli upon the intellectual abilities of the rat over a wide age range.

METHOD

Subjects

Middle-aged groups. Of 125 male white rats, 15 months old (born on the same day), obtained from Sprague-Dawley when 30 days old, 43 animals were selected which did not vary more than .5 σ from the group mean weight of 407 gm. The weight was reduced during preliminary training and held constant between 80 and 85 per cent of the original during the course of the experiment. These animals had been individually caged and had not been used on any prior experiment.

Young groups. Thirty-nine male white rats, 30 days old (born on same day), obtained from Sprague-Dawley, comprised the young group. Their weights averaged 67 gm. when received.

Both middle-aged and young rats were randomly assigned to four groups. Members of two middle-aged and two young groups were run in serial order in the morning, and the remaining four groups run in serial order in the afternoon.

Apparatus

Four copies of the five-choice Multiple Visual Discrimination Apparatus were used. One group of middle-aged and one of young rats were always run on the same-numbered apparatus. Four *E*s were rotated so that they would run each group of animals on every fourth day.

The stimulus patterns, chosen from the same ones used in a previous study (3), are shown in Figure 1. Five pairs were used in a single series. The rats learned the first two series. There were eight duplicates (photographic) of each stimulus pattern.

Procedure

All rats were first trained to jump to one card with 20-mm. vertical striae exposed with four black cards. Then 20-mm. horizontal striae were introduced and training continued with two striated cards and three black cards until 10 successive discriminations were made quickly and without error in the same day. On successive days the width of the striae was reduced through 20, 15, 10, 7.5, and 5 mm. All animals were able to make 9 out of 10 correct jumps to each of these smaller striae upon their first presentation. Eight of the older rats had to be discarded because of sickness.

On the discrimination-learning part of the experiment, five pairs of unique visual patterns were serially presented in quick succession. The rats were required to correct their mistakes. If they had not made a discrimination jump or had made an error and not corrected it in 3 min., the animals were helped. All rats were given a total of 33 repetitions of series I followed by 45 repetitions of series II.

RESULTS

Preliminary Training

The criterion of 9 out of 10 correct jumps to 20-, 15-, 10-, 7.5-, and 5-mm. vertical striae on successive days was accomplished by 35 middle-aged rats and 39 young rats. There was no significant difference in accuracy between the two age groups on any width of striae. However, when the discrimination times were compared on the 10-mm. striae the young rats were faster with a U of 1.88 (p = .028). On the 5-mm. striae this difference was still more in favor of the young rats with a U of 3.19 (p = .0006). It was evident that the older rats had a tendency to slow down as the striae were reduced in size, but the accuracy of the response was not affected. On the other hand, the younger rats were jumping more rapidly to the 5-mm. striae than they had been to the 10-mm. with no reduction in accuracy.

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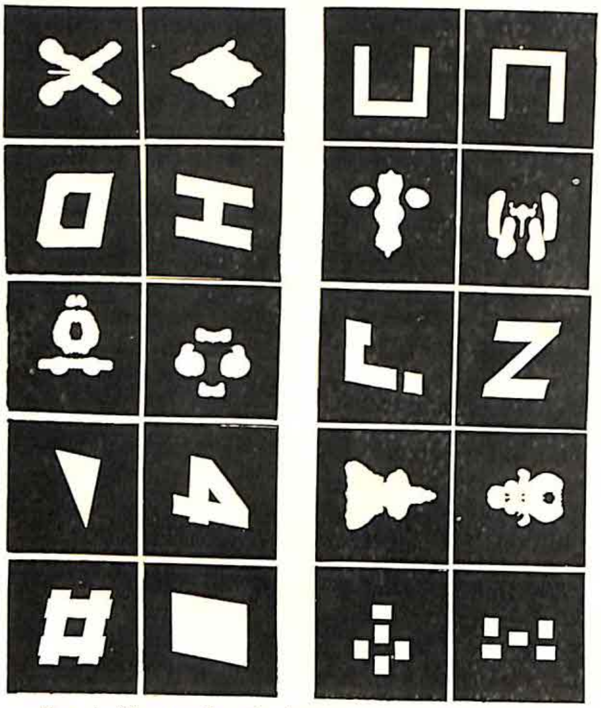

FIG. 1. Two series of stimulus cards. The cards were exposed in constant order from top to bottom. The positive card of each pair is on the left.

Learning of Series I

A total of 29 middle-aged rats finished 33 repetitions of series I, and 27 of these met all the learning criteria (9/10, 13/15, and 15/15 correct jumps). The remaining 2 were blocking and gave no indication of learning. All 39 young rats finished the training on series I, and 36 met all learning criteria in the prescribed period.

The data for the 27 middle-aged rats and the 36 young rats that had met all criteria in 165 discrimination jumps were analyzed by both parametric and nonparametric tests. The smallest difference obtained by these methods still had a probability of .002 in favor of the young rats. The U's and p values between the two groups of rats on both series I and II are presented in Table 1.

Learning of Series II

One of the 27 middle-aged rats died before completing the 45 repetitions on series II, and 17 of the remaining 26 rats failed to meet one or more learning criteria. Four of the group never met even the simplest criterion of 9 correct out of 10 jumps (two consecutive repetitions of the series). All 36 young rats completed series II. Five failed to meet one or more learning criteria, but only 1 young rat failed to meet the simplest criterion.

TABLE 1
Probability Values for Differences between Age Groups in Learning Series I and II

CRITERION	SERIES I*		SERIES II†	
	U	p	U	p
Time	5.03	.0000	4.85	.0000
9/10	3.94	.0000	0.28	.39
13/15	4.54	.0000	2.13	.02
15/15	3.49	.0025	3.65	.0001
Correct in last 50	5.54	.0000	4.50	.0000
Total C	6.46	.0000	4.72	.0000

* N = 27 middle-aged and 36 young rats.
† N = 26 middle-aged and 36 young rats.

These learning data were analyzed without excluding any rats. Where the rat did not meet a criterion, its score was the maximum number of jumps given (225). All differences between groups were significant beyond the .02 level except the number of trials before meeting the simplest criterion.

DISCUSSION

By using only rats that had met all learning criteria in the analysis of the data from series I, we were giving the benefit of any doubt to the older rats. In spite of this, the 60-day-old rats were superior in every respect to the 480-day-old rats. At 90 and 510 days of age while they were learning series II, the differences, although not so great, were always in favor of the younger rats. The younger rats also required significantly fewer helps, made fewer errors, and their ratio of errors to correct jumps was better.

The final achievement level (number correct in the last 50 jumps) was lower for both groups on the second series, and the ratio of errors to correct jumps had increased. There was also a disproportionate increase in the variability of both groups on all measures on the second series. It is believed that a part of the lowered performance efficiency may be attributed to the inclusion of more difficult pairs of stimuli (upright and inverted U) and to a change in training procedures. However, since these factors were constant for both age groups, they do not invalidate the reliability of the differences that were found.

These findings are not in agreement with Munn's summary statement that the learning ability of rats remains fairly constant from 30 days to about two years. With a more adequate separation of young (adult?) and middle-aged rats (not yet senescent) in the present study, Maier's finding that old rats were superior on intellectual functions was not supported.

SUMMARY AND CONCLUSIONS

The same group of middle-aged male rats was simultaneously tested at 450, 480, and 510 days on the identical striae and complex serial multiple-discrimination learning problems with a younger group 30, 60, and 90 days of age. There were no reliable differences between the two groups in the final accuracy with which vertical striae of five different widths were discriminated. The middle-aged rats were slower than the young ones.

When required to learn five pairs of non-logically related stimuli in a single consecutive series, the young rats were significantly superior ($p = .002$ or better) to the old ones on (*a*) total time, (*b*) number of jumps required before making 9/10, 13/15, and 15/15 correct jumps, (*c*) number correct in the last 50 jumps, and (*d*) percentage correct in the total number of attempts. The direction of the difference in learning a second series of five new pairs was the same, but the probability levels were somewhat less (not significant for 9/10; $p = .02$ for 13/15).

The use of complex multiple-discrimination learning tasks has revealed decrements in the intellectual ability of old rats which were not accompanied by significant declines in the accuracy of visual discrimination of simple striae on the jumping apparatus.

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DISCRIMINATION OF COLORED FOOD AND FOOD SIGNS BY PRIMATES

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For animals to survive they must in some way differentiate food from nonfood objects. This differentiation constitutes, in a sense, the fundamental principle underlying most methods of testing various types of discriminative ability in animals. As Lashley has pointed out: "... discrimination ... may involve a wide range of functions from a direct tropistic reaction up to the recognition of intricate logical relations subsisting among the objects compared" (7, p. 123). European students of animal behavior (9) have studied discriminative responses in animals without actually training them formally, though the possibility that the animals may have previously trained themselves exists and cannot be dismissed.

Adaptive behavior in learning consists of dropping responses which are not rewarded and maintaining those which are. One of the problems that the psychologist may study is why it sometimes takes organisms hundreds of trials to make their proper differential response in a simple discrimination situation. On the basis of experience with other species (2, 7) there is ample evidence to show that the method of training can influence the number of trials to reach a given criterion of learning. Harlow (5), in an extensive series of experiments using the Klüver form board with monkeys, has discussed some of the factors influencing the difficulty or ease of problem solution in different discrimination situations.

The present study dealt with simple color discrimination in primates, and attempted to see whether evidence of discrimination could not be obtained in a fewer number of trials than previously by changing some of the nonrelevant cues. The *relevant* cues in a color discrimination are the colors themselves, and all other aspects of the situation are *nonrelevant*.

Monkeys that have received either a few days of taming or none at all require many trials before they show evidence of simple discrimination behavior. Chow (1) trained 31 naive monkeys on a simple red-green discrimination and on a pattern discrimination (diamond versus stripes) using a modification of the Klüver form board. They took an average of 137 trials ($SD = 70$) to learn the color to a criterion of 20 errorless trials, and 154 trials ($SD = 63$) to learn the pattern. Thompson,[2] working at the Yerkes Laboratories, found that it took six chimpanzees an average of 323 trials to establish a simple black-white discrimination. These animals had solved a variety of problems for many years before this; in fact, most were born and raised in the laboratory and subject to much handling by humans. Thompson used a variation of the Klüver form board wherein the relevant cues appeared on plaques in front of the food wells, while the plaques covering the food wells did not differ appreciably from each other. In sharp contrast Lashley (7) found that it took rats an average of 6.6 trials with 0.7 errors to learn a black-white discrimination in his jumping stand.

Poor performance by an animal in a restricted situation may not represent its general ability. As Klüver has pointed out "It must be kept in mind, of course, that *negative* results do not necessarily mean that the animal is incapable of performing the response we happen to be interested in; it may simply mean that we have not set up the optimal conditions under which a given response, let us say, a certain discriminatory reaction, occurs" (6, p. 310).

In 1933, Thorndike (10) showed that simple frequency of association failed to result in learning under certain circumstances. Thorndike felt that the stimuli to be associated lacked what he called "belongingness." Though he never adequately defined the term, it would appear he meant that the *S*s were not set to see these relationships.

The following study attempted to determine whether, by changing some of the spatiotemporal relations of stimulus and reward, more or less efficient performance could be elicited from primates.

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[2] Personal communication.

METHOD

Subjects

Members of three species of primates participated in this study. They included 10 chimpanzees of varying experimental experience, 1 rhesus monkey that had worked daily for five previous months in other discrimination experiments, 1 spider monkey and 3 rhesus monkeys that had never previously taken part in psychological experiments, making a total of 15 *S*s.

Apparatus

Two blackboards each 56 cm. by 14 cm. were used to hold the stimuli. One was perfectly flat and the other had two food wells, each 5 cm. in diameter, spaced 19 cm. apart. A red and a green metal plaque each 8 cm. square were used in part of the experiment to cover the food wells. Red and green celluloid 2-cm. and 8-cm. squares were also used.

Procedure

Small pieces of bread approximately 2 cm. square were colored either red or green with vegetable dyes. Some of these were flavored with saccharine, others were unflavored, and others were rendered distasteful with a mixture of capsicum (extract of red pepper), dehydrocholic acid (extract of bile), and quinine. For some animals red was positive and green negative, and for others the reverse conditions held. Saccharine was used at first, following Franz's (3) technique, in the hope it would make the bread more desirable. But when some of the chimpanzees took a long time to eat the sweetened bread, saccharine was no longer used and subsequently the chimpanzees consumed the positive reward more rapidly.

Each animal received one pair of preliminary experiences not involving any alternative choice. The *S* was first given the positive object and always ate it, and then given the negative, which *S* invariably tasted and then threw away. It was felt that this procedure was necessary to forestall the possibility that *S* might first select the disagreeable negative object and then withdraw permanently from the situation.

The 10 chimpanzees received 20 trials, wherein the position of the positive breads was randomly arranged by the Gellermann (4) series, and they could choose either the red or green bread. Correction was allowed. Red was positive for five of the animals, and green for the other five.

The spider monkey and the sophisticated macaque were given 25 trials by the same technique. The green bread was positive for these two animals, and trials 20 to 25 were controls where both red and green breads were unflavored.

The three naive rhesus monkeys received a series of six problems with 25 trials a day. They were started the same way as the spider and the sophisticated rhesus except that red was positive for them. The second day they were switched to the conventional red-green discrimination procedure, using red and green metal plaques covering food wells, with a peanut under the red plaque. On day 3, uncolored squares of bread, flavored the same way as the original colored breads, were placed in the food wells, which were then covered with red transparent celluloid over the positive white piece of bread, and green celluloid over the negative white piece of bread. The pieces of bread were clearly visible and, of course, they *appeared* red and green respectively. The fourth day small red and green squares of celluloid the same size as the bread were pasted upon the bread. On the fifth day these celluloid squares were laid about 1 mm. in front of the white bread squares so they were between the monkey and the bread, and on the sixth day they were again placed upon the bread (though not pasted this time).

TABLE 1

Chimpanzees: Discrimination of Colored Bread

NAME	ERRORS IN 20 TRIALS	POSITIVE STIMULUS	NAME	ERRORS IN 20 TRIALS	POSITIVE STIMULUS
Art	1	Red	Mars	0	Green
Fanny	0	Green	Pan	2	Green
Flora	0	Red	Portia	2	Red
Jojo	1	Red	Rob	0	Red
Lia	0	Green	Sinbad	1	Green

TABLE 2

Monkeys: Discrimination of Colored Bread

MONKEY	ERRORS IN FIRST 20 TRIALS	ERRORS IN ADDITIONAL 5 CONTROL TRIALS	POSITIVE STIMULUS
Spider	1	0	Green
Sophisticated Rhesus	1	0	Green
Naive rhesus 1	0	0	Red
Naive rhesus 2	0	0	Red
Naive rhesus 3	1	0	Red

TABLE 3

Monkeys: Color Discrimination with Various Techniques

Error in 25 Trials

SUBJECT	COLORED BREAD (0–25 Trials)	CONVENTIONAL (26–50 Trials)	TRANSPARENT STIMULUS (51–75 Trials)
Naive 1	0 (0%)	14 (56%)	11 (44%)
Naive 2	0 (0%)	13 (52%)	9 (36%)
Naive 3	1 (4%)	15 (60%)	12 (48%)

SUBJECT	PASTED STIMULUS (76–100 Trials)	ADJACENT STIMULUS (101–125 Trials)	COVERING STIMULUS (126–150 Trials)
Naive 1	0 (0%)	11 (44%)	0 (0%)
Naive 2	0 (0%)	10 (40%)	0 (0%)
Naive 3	0 (0%)	12 (48%)	0 (0%)

The animals received all the training in their home cages.

RESULTS

Results for the chimpanzees can be seen in Table 1. Five of them made no errors in 20 trials, three made 1 error, and two made 2 errors. It must be remembered that these animals all received one preliminary experience which revealed to them the nature of the stimuli. Learning was essentially in one trial.

Table 2 shows the results of the same experiment with monkeys. Two of the naive monkeys made no errors and the other three monkeys made one error each in the first 20 trials. In addition they received five control trials where both red and green breads were unflavored. Like the chimpanzees, they learned in a single trial. None of the monkeys made any errors (that is, chose the originally negative bread) in the control trials.

Table 3 shows what the three naive monkeys did on the remaining tasks. On the first day with colored bread they consistently chose the red bread. The second day they were switched to a conventional red-green discrimination to see if they would transfer their predominant choice of red. Not only did they not transfer, but if anything they chose slightly in the opposite direction.

On the third day, white pieces of bread were placed in the food wells and covered with the red and green pieces of celluloid. While performance is slightly better on this day, it is still not very far from chance. Note that here the animals saw red and green pieces of bread just as they did on day 1. Perhaps their inferences about color constancy were interfering with their performance.

On the fourth day small squares of celluloid the same size as the bread were pasted to the bread. Again visible to the animals were red and green squares of bread, and not one monkey made a single error in 25 trials. The following day, instead of covering the bread, the celluloid was laid next to it. With this the scores reverted to chance.

On the sixth day the procedure of the fourth day was repeated, but this time the plates were only laid upon the bread, not pasted to it. Again there were no errors.

DISCUSSION

These results may have some practical significance for the training of primates in visual discriminations, and theoretical significance regarding the nature of perception and attention in these animals.

There is no record in the previous literature of such rapid color discriminations in naive primates, with the possible exception of Franz's work. It seems clear to this author that inducing learning sets for displacing stimuli covering food wells is not the only way to get rapid discrimination of relevant stimuli.

CONCLUSIONS

The results show that the animals could very quickly see the relation between the relevant stimuli and the reward when presented with the situation in a certain way. They are able to see the relation between proper color and reward within a few trials with colored bread, but only after a great many trials with colored plaques. While the present experiment does not examine the parameters involved in detail, it suggests that spatial and temporal proximity of cue to reward may play an important role in rapidity of discrimination.

In summary, this experiment demonstrated that experimentally naive primates could make color discriminations after only one or two trials, whereas the usual techniques, utilizing the Klüver form board, require relatively long periods of training.

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PERCEPTUAL DIFFERENTIATION IN THE COURSE OF NONDIFFERENTIAL REINFORCEMENT

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From the assumption that habit strength grows as a negatively accelerated function of the number of reinforcements, it follows that the rate at which a difference in strength between competing response tendencies develops should be inversely related to the initial strengths of the separate tendencies. In his latest volume Hull has worked out this deduction for a simple trial-and-error situation in which "The two stimuli . . . are very similar and the responses . . . are different though they often involve substantially the same muscles" (4, p. 23).[1] Hull analyzes two hypothetical examples, Case I (${}_{S}E_{R+} = {}_{S}E_{R-} = 2.5\sigma$) and Case II (${}_{S}E_{R+} = {}_{S}E_{R-} = 4.5\sigma$); his computations show that 25 trials are required to reach a .978 dominance of ${}_{S}E_{R+}$ in the second case as compared with only 10 trials in the first. Evidence in support of this deduction has been provided by Siegel (9) in an experiment with rats in a T maze and by Maltzman and Morrisett (7) in an experiment on the solution of anagrams by human *S*s. As Siegel noted, such data are difficult to reconcile with the concept of perceptual learning, since increased experience with a situation should, all other things equal, provide greater opportunity for perceptual development. It may be noted, however, that in both these experiments *S*s were confronted primarily with problems of response selection. The experiments to be reported here involved a discriminative situation in which the primary task was perceptual differentiation.

EXPERIMENT I

Method

Subjects. Thirty naive albino rats bred in the laboratory from Wistar stock were studied. The animals were between three and four months old at the beginning of the experiment.

Apparatus. A conventional two-window Lashley jumping stand was employed. Behind the windows was a feeding platform, and below them was a cloth net into which the animals fell after each incorrect response. The entire apparatus was painted flat black. The stimulus cards used in the experiment were as follows: two homogeneous mid-gray cards, and four black-and-white striped cards (stripe width $= \frac{1}{2}$ in.) of which two were vertically and two horizontally striped.

Preliminary training. The animals were maintained on a 24-hr. feeding schedule throughout the experiment. During the first week of training they were handled and fed on the feeding platform of the apparatus. Then they were taught to jump gradually increasing distances (to a maximum of 9 in.) from the jumping platform to the open windows. Manual guidance was employed to ensure equal experience with both windows. At the conclusion of the preliminary training the animals were divided into three groups of ten each which were matched for flexibility displayed in the open-window situation.

Stage I. In the first stage of the experiment all animals were given 12 reinforced trials per day for a period of 10 days. For group I the gray cards were used, and manual guidance was employed to ensure an equal number of reinforcements for responses to each window. Groups II and III were trained with the horizontal and vertical cards, but for group II the cards were presented in successive configurations (either two horizontals or two verticals on each trial) while group III was trained with simultaneous configurations (either vertical-horizontal or horizontal-vertical on each trial). The number of reinforcements on each card and each window was equated by manual guidance. For each animal in each of the three groups half the trials were free and half forced, and each jump was rewarded with a nibble of wet mash.

Stage II. Following the ten days of nondifferential reinforcement in Stage I, all animals were trained on a simultaneous discrimination between horizontal and vertical cards. For half the animals in each group the vertical card was positive, while for the remaining animals the horizontal card was positive. The position of the positive card was alternated in accordance with selected Gellermann orders (3). Ten trials per day were given by the correction method. Each trial consisted of a series of one or more jumps terminating with a correct response. The animal was permitted a maximum of three errors on any trial, after which it was manually guided in the correct direction. The criterion of learning was two successive errorless days.

Results

In Figure 1 the course of learning in the three groups is plotted in terms of initial errors. The curves show comparable rates of learning in groups I and II, while group III learns more rapidly than either of the other two. In Table 1 the results for the three groups on the horizontal-vertical problem are summarized in terms of three measures: initial errors, total errors, and days. Differences among the groups were statistically evaluated in terms of Wilcoxon's test for unpaired deviates (13). No significant differences appeared between groups I and II in terms of any of the three scores. Group III made significantly fewer initial and total errors than did group I ($p < .01$), and its performance was superior to that of group II in terms of all three measures ($p < .01$).

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[1] The same logic applies to cases in which either the two stimuli or the two responses are identical.

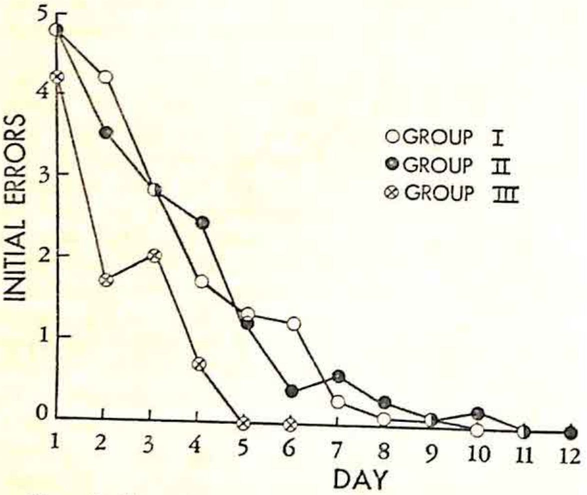

FIG. 1. Learning curves for the three groups of Experiment I (simultaneous horizontal-vertical discrimination)

TABLE 1
Learning Scores for the Three Groups on the Simultaneous Horizontal-Vertical Discrimination (Experiment I)

SCORE	GROUP		
	I	II	III
Mean initial errors	16.4	16.6	8.6
Mean total errors	30.3	27.7	14.4
Mean days	7.2	8.0	5.0

Discussion

These results fail to support predictions made from the concept of a continuous, negatively accelerated growth of habit strength as a function of frequency of reinforcement. From that concept it would be deduced (*a*) that groups II and III should perform equally well (since both had received the same number of reinforcements on each card in each position during Stage I) and (*b*) that the performance of group I (which had not been previously reinforced on the striped cards) should be better than that of the other two groups. Neither deduction was confirmed.

The superiority of group III as compared with group I suggests that a significant amount of perceptual differentiation occurs in the absence of differential reinforcement. This result represents an extension of Lawrence's findings on the "acquired distinctiveness of cues" (5, 6), although it cannot be explained in terms of the theoretical formulation proposed by Lawrence—the components discriminated by group III in Stage II were not differentially reinforced in Stage I, nor were they constituents of differentially reinforced compounds.

The superiority of group III as compared with group II and the lack of a significant difference between groups II and I, taken together, suggest that the differentiation which took place in group III was largely configurational in character (11, 14). In his latest work, Hull (4, p. 94) has considered the hypothetical operation of process-trace compounds in two-choice as contrasted with one-choice discriminative situations, but the configurational effects here obtained cannot be accounted for in these terms. Since the process-trace compounds differentially reinforced in the second stage of the experiment (i.e., horizontal process compounded with vertical trace and vertical process compounded with horizontal trace) had greater initial strength for group III than for group II, a *positively* accelerated growth of habit strength would have to be postulated to account for the superiority of group III.

In order to provide more general information on the configurational effects studied in the first experiment, a second experiment was undertaken in which animals were trained as before but tested with a successive discrimination. For the purpose of more effective comparison of the results, the two studies ran concurrently, and the animals employed in both were drawn from the same litters.

EXPERIMENT II

Method

Subjects. Thirty naive albino rats bred in the laboratory from Wistar stock were studied. They ranged in age between three and four months at the beginning of the experiment.

Apparatus and procedure. The conditions of Experiment II were identical with those of Experiment I except that all groups were trained on a successive horizontal-vertical discrimination in the second stage. The numbers of the three new groups correspond functionally with those of the first three; that is, the two sets of numbers designate similar relations between Stage I and Stage II conditions. Thus, in the second experiment group I was shifted from grays to the successive stripe discrimination; group II from simultaneous presentation to the successive discrimination; and group III from successive presentation to the successive problem.

Results and Discussion

The course of learning in the three groups, plotted in terms of initial errors, may be seen in Figure 2. These curves show the same general trends as do those of the previous experiment (Fig. 1). Mean scores for the three groups (initial errors, total errors, and days) are shown in Table 2. Again in the second experiment there were no significant differences between groups I and II, while group III made significantly fewer initial errors ($p < .01$) and total errors ($p < .02$) than did group I. In the second experiment, unlike the first, however, the performance of groups II and III did not differ significantly, although the differences were in the same direction (just short of the .05 level for both initial errors and total errors by Wilcoxon's nonparametric method). The skewed error distributions did not warrant use of a more sensitive test.

Because of the similarity between the results of the two experiments, the two sets of data were combined to provide a more general picture. In Table 3 the results for combined groups are summarized in terms of the three indices of learning. The performance of the combined group III is significantly superior ($p < .01$) to that of each of the other two groups as measured by initial errors, total errors, and days. The performance of the combined groups I and II differs significantly ($p < .05$) only in total errors, the performance of group II being superior in this respect. As has already been noted in connection with the results of the first experiment, these differences contradict the assumption of a negatively accelerated growth of habit strength as a function of frequency of reinforcement—apparently nondifferential reinforcement facilitates rather than retards perceptual differentiation. That this differentiation is dominantly configurational is evidenced by the significant differences between groups II and III, which were equated for frequency of reinforcement on the two striped cards. The difference between groups I and II in terms of

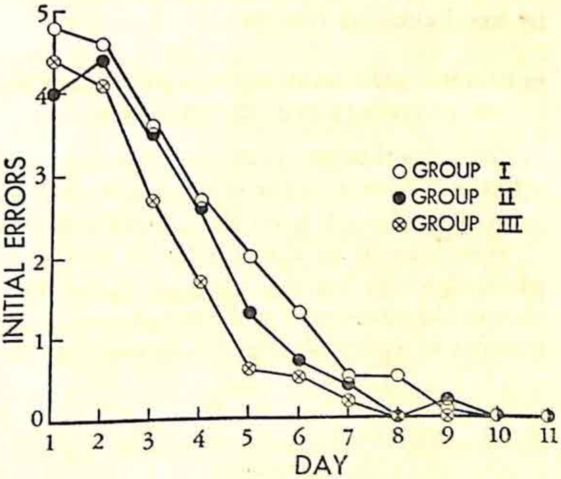

Fig. 2. Learning curves for the three groups of Experiment II (successive horizontal-vertical discrimination)

TABLE 2

Learning Scores for the Three Groups on the Successive Horizontal-Vertical Discrimination (Experiment II)

SCORE	GROUP		
	I	II	III
Mean initial errors	20.0	17.9	14.2
Mean total errors	34.9	28.8	22.4
Mean days	8.6	7.9	7.1

TABLE 3

Learning Scores for Combined Groups (Experiments I and II)

SCORE	GROUP		
	I	II	III
Mean initial errors	18.20	17.25	11.40
Mean total errors	32.60	28.25	18.40
Mean days	7.90	7.95	6.05

total errors suggests, however, that some horizontal-vertical differentiation may develop independently of configuration in the course of nondifferentially reinforced experience with the cards. These findings require a theoretical approach quite different from that provided by neo-Pavlovian theory.

SUPPLEMENTARY FINDINGS ON SIMULTANEOUS VS. SUCCESSIVE DISCRIMINATION

The experiments thus far reported and additional tests with the same animals provide some interesting data on the relative difficulty of simultaneous as compared with successive discrimination. Spence (10) accounts for solution of the successive problem in terms of the concept of compounding and is therefore led to the conclusion that the successive problem must be more difficult than the simultaneous. Although this conclusion is supported by the results of some experiments from Spence's laboratory, the experimental conditions employed in two other recent experiments have led to precisely the reverse outcome, i.e., greater difficulty of the simultaneous problem (2, 12).

TABLE 4

Relative Difficulty of Two Simultaneous and Successive Problems

	MEAN INITIAL ERRORS	
	Horizontal-Vertical	Circle Size
Simultaneous	13.9	12.2
Successive	17.4	12.8
Diff.	3.5*	.6

* Significant beyond the .01 level of confidence by the nonparametric Mann-Whitney U test (8).

Since the present experiments differed only in the second stage—the animals were trained on a simultaneous problem in Experiment I and on a successive problem in Experiment II—they provide additional data on the relative difficulty of the two types of problem. Although the performance of each group of Experiment I was superior to that of the corresponding group of Experiment II, only the difference between the III groups was statistically significant ($p < .01$) by Wilcoxon's test for unpaired replicates (13). As may be seen from Table 4, when the three groups of each experiment are combined, the animals of Experiment I are found to make significantly ($p < .01$) fewer errors on the simultaneous problem than do the animals of Experiment II on the successive problem.

When each animal had reached criterion on the horizontal-vertical discrimination, it was trained by the same method on a discrimination between two circles (white on black grounds) differing in diameter (1 in. and 4 in., respectively). The animals which had previously learned the simultaneous stripe problem (Experiment I) were trained on the simultaneous circle problem. Those which had previously learned the successive stripe problem (Experiment II) were trained on the successive circle problem. The performance of the two groups on the circle discrimination is plotted in Figure 3. As may be seen from Table 4, the difference in error scores did not approach significance. This result may be understood in terms of the operation of qualitatively distinct levels of perceptual organization in two-choice problems (2). Although within-pairs, as compared with between-pairs, differentiation seems to be facilitated in situations requiring direct approach to the stimulus objects—which accounts for the initially greater difficulty of the successive problem—the difference between the two kinds of problem disappears after a

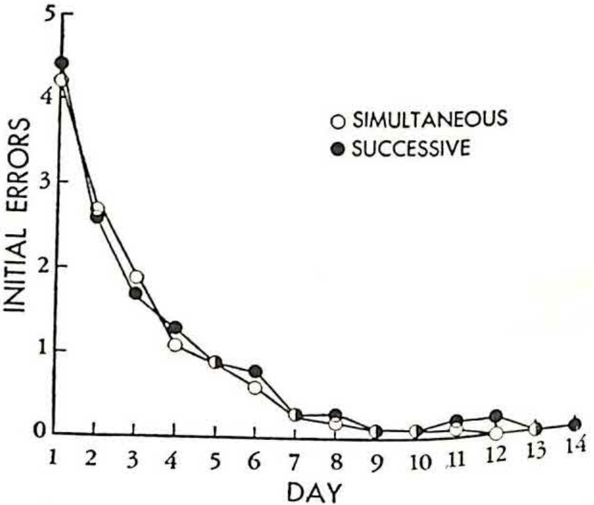

FIG. 3. Learning curves for the combined groups of Experiment I (simultaneous circle-size discrimination) and for the combined groups of Experiment II (successive circle-size discrimination)

between-pairs set has been established. The present findings may be added to the list of others (1) which fail to support Spence's theory.

SUMMARY

Three groups of rats were trained in a two-window jumping apparatus for a period of ten days during which time all jumps were rewarded. One group was trained with a pair of identical mid-gray cards, while the others were trained with horizontally and vertically striped cards. Of these groups, one encountered the cards in simultaneous configurations (horizontal-vertical and vertical-horizontal) and the second experienced the cards in successive configurations (horizontal-horizontal and vertical-vertical). In Experiment I half of the animals in each group then learned a simultaneous discrimination between the striped cards, and in Experiment II the remaining half of the animals learned a successive stripe discrimination. The following results were obtained: Animals trained on one set of stripe configurations and tested on the other made significantly fewer total errors than did the animals trained on gray cards. Animals trained and tested on the same configurations were markedly superior to the other two groups in terms of all measures of performance. These results fail to support predictions based on the assumption of a negatively accelerated growth of habit strength as a function of frequency of reinforcement. Supplementary findings on the relative difficulty of simultaneous and successive problems are reported.

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THE ROLE OF GENERALIZED APPROACH AND AVOIDANCE TENDENCIES IN BRIGHTNESS DISCRIMINATION

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The major purpose of the present study was to verify a specific deduction concerning the role of generalized approach and avoidance tendencies in brightness discrimination learning. In a discrimination problem of the simultaneous cue presentation type, any condition which prevails to facilitate choice of the positive cue and rejection of the negative cue should promote more rapid discrimination. Similarly, any condition which prevails to facilitate rejection of the positive cue and choice of the negative cue should retard discrimination until the effects of that condition have been overcome. The present study concerns the role of primary stimulus generalization under conditions which facilitate and retard discrimination learning according to the above two possibilities.

The theoretical expectations derive from three assumptions. The first of these concerns the acquisition of the capacity to elicit approach behavior by a neutral stimulus. Accordingly, whenever a neutral stimulus, e.g., one which elicits neither approach nor avoidance behavior consistently, is repeatedly experienced in close association with reward, the stimulus acquires the capacity to elicit approach behavior. The assumption is essentially Hull's (1) principle according to which neutral stimuli acquire the property to function as secondary reinforcers. A distinction, however, should be made in the possible functions of such stimuli in behavior situations. Where the stimulus functions to establish and strengthen new S-R associations, it may be said to play a reinforcement role. Where the stimulus functions to elicit approach behavior only, it may be said to play a derived-incentive role. Such stimuli need not fulfill both functions in all situations.

The second assumption concerns the acquisition of the capacity to elicit avoidance behavior by a neutral stimulus. Accordingly, whenever a neutral stimulus is repeatedly experienced in close association with frustrative nonreward, the stimulus acquires the capacity to elicit avoidance behavior. Finally, Hull's (1) principle of primary stimulus generalization, somewhat modified, provides the third assumption. Stated generally, the assumption is this: to the degree that other stimuli are similar to stimuli that have acquired the capacity to elicit either approach or avoidance, to that degree will they also elicit either approach or avoidance.

From these assumptions it follows that if the positive cue is similar in brightness to the reward goal box, in which drive reduction in the form of food reward is experienced, and if the negative cue is similar in brightness to the nonreward box, in which drive intensification in the form of frustrative nonreward is experienced, the positive and negative cues will elicit approach and avoidance tendencies respectively. It follows that discrimination learning should be facilitated. In a similar manner, if the positive cue is similar in brightness to the nonreward box and the negative cue is similar to the brightness of the reward goal box, the positive cue will elicit, for a time at least, avoidance tendencies, and the negative cue will elicit, for a time at least, approach tendencies. Relative to the first condition, discrimination learning should be retarded.

The primary purpose of the study was to test this deduction. A secondary purpose was to obtain data pertinent to the continuity-noncontinuity issue in a more direct manner than that involved in previous studies related to this issue.

METHOD

Subjects

The *S*s were 20 female, hooded rats from the colony of the department of psychology and education at the Carnegie Institute of Technology. They ranged in age from 90 to 120 days at the beginning of the experiment.

Apparatus

The apparatus consisted of two units, a straight runway used during preliminary training and a single-unit T maze used during the discrimination training. A sketch of the T maze is presented in Figure 1.

The T maze was constructed of wooden pathways and walls, and covered with panels of Plexiglas. A guillotine-type door separated the starting box from the stem of the maze. The arms of the maze consisted of two transversely sliding units with three separate runways, painted flat black, medium gray, and gloss white, respectively. These stem units could be manipulated so that any one of the three differentially painted runways would be in position between the maze choice point and the entrance of either goal box. A second guillotine-type door was located at the choice point. It was constructed in the form of an inverted T, with the flat back of the T facing the stem runway. It prevented the *S*s from retracing the maze after a choice-point response.

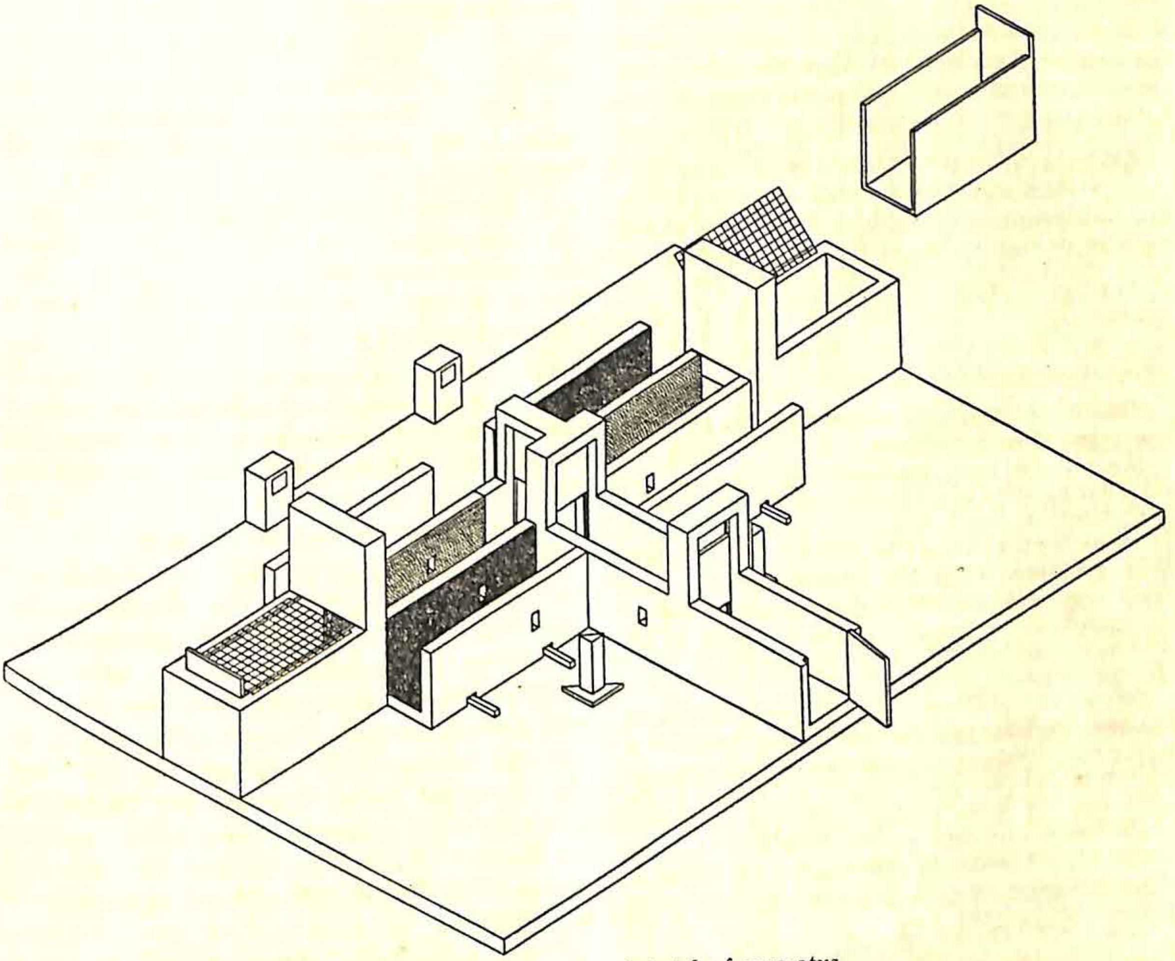

FIG. 1. Three-dimensional sketch of apparatus

The end boxes consisted of two units, an outer shell detachable from the arms of the maze, and a plywood insert which functioned as the goal box proper. The shell interiors were unpainted, and the interiors of the inserts were a flat black and a gloss white, respectively. This shell-insert construction in combination with the transversely sliding arm units enabled the *E* to arrange rapidly various combinations of arm pathway to goal-box brightnesses on either side of the choice point.

Deep-grooved, guillotine-type doors were built into the goal boxes and faced the arm runways. During discrimination training, these doors were opened only after a choice-point response had been made in order to prevent the differentiated interiors of the goal boxes from influencing a choice-point response. The goal boxes were covered with panels of hardware cloth.

Maze illumination was provided by five 100-w. lights located 3 ft. above the arm and goal-box units of the maze. A one-way vision screen separated *E* from the maze.

A photoelectric beam was so angled that it cut across one of the arm units, continued across the stem pathway approximately 1 in. from the starting-box door, and then cut across the second arm unit. This arrangement enabled *E* to time the interval between entry into the stem pathway and entry into one of the arm cue alleys. Interruption of the stem beam caused a clock to start, and interruption of either arm beam stopped the clock.

Preliminary Training

All *S*s were placed on a 23-hr. food-deprivation schedule five days before preliminary training began. This schedule was maintained for the duration of the experiment. Preliminary training began in the straight runway. All *S*s were given five food-reinforced trials per day for six successive days. The purpose of this phase of the training was to acquaint the *S*s with the goal-box environment and to establish a running-for-food habit.

Preliminary training continued in the T maze. All *S*s were given five forced trials per day to each goal box on the seventh and eighth days. The *S*s were run through the neutral gray arm pathway into the unpainted end boxes. All trials were food reinforced. A single-alternation pattern was used. The pattern was so initiated that the last forced trial on the eighth day was to the side opposite that which was correct for the first discrimination-training trial. The purpose of this phase of the training was to acquaint the *S*s with the static conditions of the T maze and to provide an equal number of food-reinforced experiences with both end boxes.

Discrimination Training

The *S*s were randomly assigned to the following four experimental groups:

Group I. The discrimination required *S*s to choose the white pathway which led to food reinforcement in the white goal box in preference to the alternative black pathway which led to no food reward in the black goal box. Thus, the brightness of the food-reward goal box was essentially the same as that of the positive-cue pathway, and the brightness of the nonreward goal box was the same as that of the negative-cue pathway.

Group II. The discrimination problem required *S*s to choose the black pathway which led to food reward in the black goal box in preference to the alternative white pathway which led to no food reward in the white goal box. Thus, as with group I, the brightness of the food-reward goal box was essentially the same as that of the positive-cue pathway, and the brightness of the nonreward goal box was the same as that of the negative-cue pathway.

Group III. The discrimination problem required *S*s to choose the white pathway which led to food reward in the black goal box in preference to the black pathway which led to nonreward in the white goal box. Thus, unlike the condition prevailing for groups I and II, the brightness of the food-reward goal box was essentially the same as that of the negative-cue pathway, and the brightness of the nonreward goal box was the same as that of the positive-cue pathway.

Group IV. The discrimination problem required *S*s to learn to choose the black pathway which led to food reward in the white goal box in preference to the white pathway which led to nonreward in the black goal box. Thus, again unlike the condition prevailing for groups I and II, the brightness of the food-reward goal box was essentially the same as that of the negative-cue pathway, and the brightness of the nonreward goal box was the same as that of the positive-cue pathway.

Except for the above conditions, the procedure was the same for each of the four groups. Running under a 23-hr. food-deprivation schedule, all *S*s were given 10 trials per day, for which the correct food-containing goal box was located successively L (left), R (right), R, L, L, R, R, L, L, R. On alternate days the mirror image of this pattern was employed.

A choice was defined as body-length entry into an arm pathway. Correction was not permitted. If correct, the *S*s were allowed 20 sec. to consume the pellet of food before being returned to the intertrial waiting cages. If incorrect, they were detained for the same time period in the nonreward goal box. The intertrial interval of approximately 5 min. was used. The criterion of learning was 18 correct trials out of a block of 20. A block of 20 trials was defined as the 20 trials involved in two successive days' training.

Although a learning criterion was adopted, all *S*s were given 50 trials beyond the point of first reaching criterion performance. Upon the completion of these 50 additional trials, the discrimination problem was reversed for each *S*. Accordingly, the heretofore positive-cue alley led to no reward, whereas the heretofore negative-cue alley led to food reward. Training continued until the criterion of 18 correct trials out of a block of 20 was reached. All trials during the reversal phase were timed to approximate choice time. The time data are relevant to the continuity-noncontinuity issue.

RESULTS AND DISCUSSION

The mean number of trials to criterion for the combined groups I and II, for which the brightness of the food-reward goal box was essentially the same as that of the positive-cue alley, and the brightness of the nonreward box was essentially the same as the brightness of the negative-cue alley, was 35.0. The mean for the combined groups III and IV, for which the brightness conditions were the converse, was 86.0. A *t* approximation test described by Snedecor (3, p. 83) indicated the difference to be significant between the .01 and .02 levels of confidence ($t = 3.02$). The results are according to theoretical expectation. Presumably, the brightnesses of the reward and nonreward end boxes acquired approach- and avoidance-eliciting value, respectively, as a result of association with conditions of need reduction and frustration, respectively. The approach- and avoidance-eliciting properties then generalized to similar brightnesses in the cue alleys. The resultant condition favored approach to the positive-cue alley and avoidance of the negative-cue alley by groups I and II, thereby facilitating discrimination learning. For groups III and IV, the resultant condition favored avoidance of the positive-cue alley and approach to the negative-cue alley, thereby retarding discrimination learning.

The results are significant for methodological as well as theoretical reasons. They indicate how choice-point behavior may be influenced by generalized approach and avoidance tendencies. Such conditions may prevail in discrimination studies without the knowledge of the experimenter. It has been observed, for example, by Hull (2) and others that when the positive cue is brighter than the negative cue, discrimination proceeds more rapidly than when the reverse brightness relationship prevails. The observation provides, in part, the basis for Hull's stimulus intensity dynamism construct. It is a characteristic condition of these studies, however, that the brightness of the reward goal box is more similar to the brightness of either the positive or negative cue. Depending upon the nature of the brightness similarity relationship, discrimination learning may be either facilitated or retarded, according to the theoretical interpretation above.

The results also have a bearing on the "relational" vs. "specific stimulus" issue in discrimination theory. The former essentially interprets discrimination learning as reaction not to the specific properties of the stimuli to be discriminated, but to the relationships inherent in the total stimulus complex. The latter stresses reactions to the specific properties of the stimuli to be discriminated. In the present study, the brightness relationship between positive- and negative-cue alleys was constant for all groups. The results are consequently not in accord with "relational" theories of discrimination learning as presently formulated.

The data obtained from the reversal training concern the continuity-noncontinuity issue. During reversal training, the *S*s went through three distinct phases. In the first phase, all *S*s continued to choose, as one would expect, the heretofore positive-cue alley, which led to no reward under the reversal condition. This phase terminated abruptly into a position habit phase which, when broken, was followed quickly by criterion performance. (It is what occurred during the position habit phase that bears on the continuity-noncontinuity issue.)

The reader will recall that running times were clocked in a manner to approximate choice-point times. Thus, during the position habit phase, there were running times for the trials on which the *S*s ran through the incorrect-cue alley and through the correct-cue alley. A comparison of these two kinds of running times is shown in Figure 2. The two gradients consist of the median values for the running times, taken in blocks of two trials, for the trials which preceded the position habit break. The latter was defined as the first run which broke a beyond-chance succession of position runs. The solid line gradient shows a gradual increase in running times for the nonrewarded runs of the position habit. The highest point of this gradient represents the median running time for the two incorrect runs just preceding the position habit break; the next point represents the median value for the two previous incorrect runs, and so on until all the points are covered. The dashed-line gradient shows a tendency toward a decrease in the running times for the rewarded runs of the position habit. The significance of these two gradients is that the continuity of the discrimination process becomes directly apparent when instead of observing the correctness or incorrectness of the response, a more sensitive response measure, as choice time, is observed. The results are more in accord with

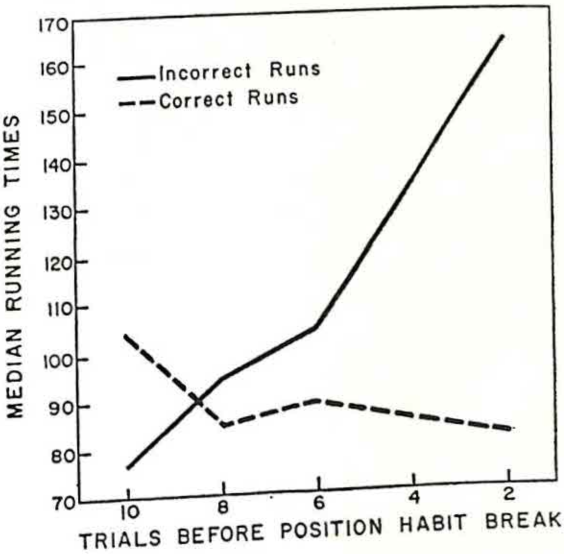

FIG. 2. Running times during position habit performance

"specific stimulus" discrimination theories of the type first formulated by Spence (4), which imply the continuity point of view.

SUMMARY

The purpose of the study was to verify a specific deduction concerning the role of generalized approach and avoidance tendencies in brightness discrimination learning. A group of *S*s for which the brightness of the positive cue was similar to the brightness of the reward goal box and for which the brightness of the negative cue was similar to the brightness of the nonreward goal box learned the brightness discrimination more rapidly, in accordance with theoretical expectation, than a group of *S*s for which the brightness of the positive cue was similar to the brightness of the nonreward goal box, and for which the brightness of the negative cue was similar to the brightness of the reward goal box.

Analysis of the running times of the *S*s during reversal training concerned the continuity-noncontinuity issue. The data gave direct support to the continuity point of view rather than support by inference, as has been the case of reversal training studies designed for this theoretical issue.

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A GRADIENT OF REINFORCEMENT OBTAINED FROM A COMPLEX DISCRIMINATION PROBLEM

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A gradient obtained by Perin (11) with the effects of secondary reinforcement substantially reduced reached zero at 34 sec. This was termed the "gradient of reinforcement" by Hull (8), who made a distinction between these results and those obtained in the studies of Hamilton (5) and Wolfe (14). The latter retained the "goal gradient" term of Hull's earlier formulation (7).

Much of the recent work in this area has been done under the direction of Spence. In an analysis of the problem Spence (13) concludes that secondary reinforcement has not been adequately eliminated in previous studies. For example, the lever-pressing response in Perin's study (11) was sufficiently different from other responses that proprioceptive cues from it could become secondarily reinforcing.

An early Iowa study on this problem is that of Perkins (12) using a T maze. The floor and top of the maze were constructed of opal-flashed glass. External cues were controlled by randomizing the position of the delay boxes. But according to Spence (13), learning could have been on the basis of proprioceptive cues.

A more direct development of the Spence point of view is found in an experiment of Grice (4) using a discrimination box with the entrance to the alleys painted black or white. Each stimulus color appeared equally often on each side. The gradient obtained is very short, becoming asymptotic at approximately 10 sec. Grice (4) concluded that the visual stimulus trace of the black and white may have been differentially rewarding.

The discrepancy between the gradients of Grice (4) and Perin (11) and the hypotheses of Hull (8) and Spence (13) indicates the need for further information regarding this principle. The present study was designed to provide additional data on the gradient obtained under conditions providing no differential secondary reinforcers. The method used was recently developed by Heron (6) and is believed to provide better control of secondary reinforcement than has been used heretofore. It not only meets the Spence (13) criterion but goes further by using each stimulus as positive and negative cue, thus negating Grice's (4) criticism in so far as it applies to this study. The method consists of learning a black-white discrimination simultaneously with the discrimination of internal stimuli and will be described in detail later.

METHOD

Animals

Forty-eight female albino rats of the Sprague-Dawley strain were used. The average age at the beginning of the experiment was 100 days (range 85 to 110). They were divided into four groups of 12 each and were delayed 0, 5, 10, and 20 sec., respectively. A criterion of learning which corresponded to 90 per cent (nine or more correct responses for four consecutive days) was to be used and was reached by 1 animal in the 0-, 5-, and 20-sec. groups and by 2 in the 10-sec. delay group. Three other animals were eliminated because of sickness. Since so few animals reached the criterion, it was decided to run the remaining 40 animals for a total of 1,000 trials each, regardless of proficiency. There were 11, 10, 8, and 11 such *S*s in the delay groups 0, 5, 10, and 20 sec., respectively.

Apparatus and Procedure

The apparatus consists of a Y-shaped maze with the arms formed of delay and goal alleys. The rat was placed in the stem of the Y from which it passed to the choice point. From this point it passed under either a white or black curtain which was hung ½ in. in front of the doors to the delay alleys. The two curtains were removable so that their position could be changed. All alleys are 3½ in. wide (inside dimension) and painted a neutral gray. There are vertical sliding doors to set the delay alleys off from the rest of the maze. The stem of the Y is covered with screen, the choice chamber with clear glass, and the delay and goal alleys with frosted glass. A 10-w. electric bulb 20 in. above the choice point provided the only illumination in the experimental room.

Five days before the experiment proper, the animals were placed on a 24-hr. maintenance schedule, receiving food and water only once each day.

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[1] A thesis submitted in partial fulfillment of the requirements for the Master of Arts degree, University of Minnesota. The author wishes to express his appreciation to Dr. W. T. Heron, under whose direction the study was done.

Preliminary training consisted of exploring a straight path resembling the maze for 5 min. a day for three days.

When white was to be the positive stimulus during the learning trials, water was placed in the living cages, and when black was to be the positive stimulus, food was placed in the living cages 1 hr. before the day's trials were to be run. On days of water deprivation, a black choice was rewarded with water, and on days of food deprivation, a white choice was rewarded with food. The position of the white and black stimulus curtains and the days of food or water deprivation were varied according to a prearranged sequence (abaababbab, abbabaabab, or ababbabaab). The first correct trial of the day appeared equally often on each side. The animals were run ten trials a day and received either food or water, never both, on completion of the day's run. The food was ground Purina Chow mixed with just enough water, approximately 1 cup per pound of dry food, to hold it together and permit swallowing. When the food was changed from one goal box to the other, the spilled food was carefully removed with a damp cloth to prevent the rat from obtaining reinforcement. Although the food was removed, the odor remained so that both goal boxes smelled of food. The work done in olfactory discrimination indicates that a discrimination of the minute intensity difference here involved is extremely doubtful.

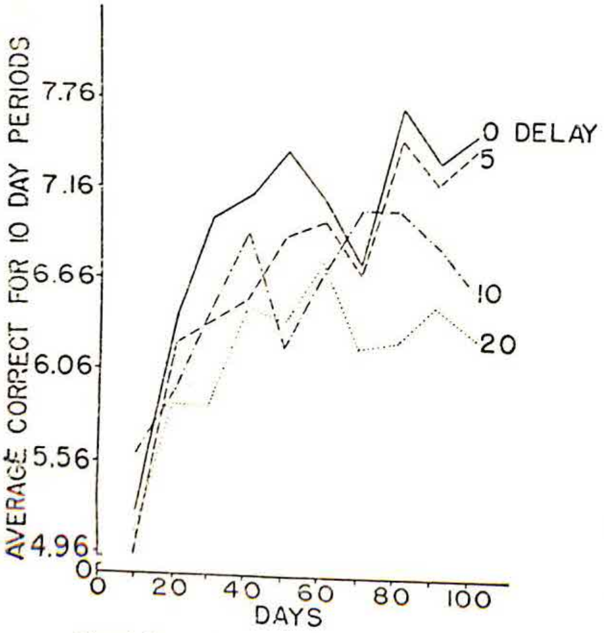

FIG. 1. Learning curves for the four groups

The noncorrection method was used, and the trials were separated by the time required to run the rest of the group. This varied from approximately 6 min. for the zero delay group to 12 min. for the 20-sec. delay group. The animal was considered to have made a response when the door to the delay compartment could be lowered behind *S*. Following the specified delay, the door to the goal box was raised, and the animal was allowed to enter and remain in the goal box for approximately 2 sec. The time spent with the food in the goal box was set only as the time required for removal. When checked by a second individual, the time was found to vary less than ½ sec. For the zero delay group the door to the goal box remained closed until a turn had definitely been made at the choice point.

RESULTS

The learning curves presented in Figure 1 reveal a tendency for the means to differ in the expected direction in spite of large day-to-day variations.

A typical hunger and thirst curve is presented in Figure 2 as an example of the relative performance on hunger and thirst days. All groups did almost consistently better under hunger than under thirst motivation. An explanation in terms of simple interference is rejected because the difference is consistently in the same direction, which could not result through interference alone. It seems more logical to assume that the use of slightly moistened food to reduce hunger reduced the thirst drive to a small degree, thereby, according to Hullian theory, lowering the excitatory potential and, consequently, the effective reaction potential on thirst days as compared with hunger days. A later study could presumably offset this methodological problem by increasing the period of thirst deprivation relative to food deprivation.

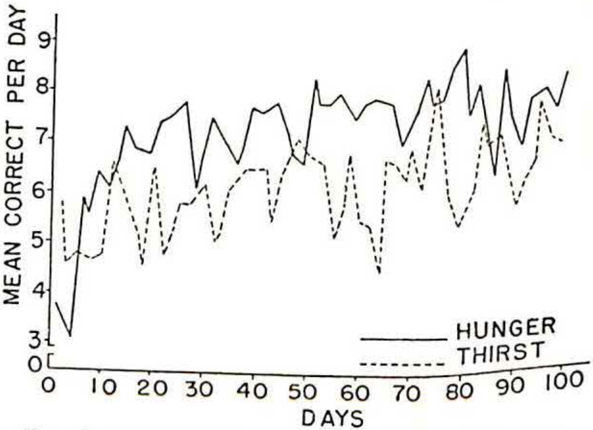

FIG. 2. Learning curves of the 5-sec. delay group acquired with deprivation of food or water

The results of an analysis of variance (1) of the data are presented in Table 1. Each *F* is significant beyond the .01 level. We can conclude, therefore, that the experimental variable (delay difference) has produced significance between groups; that learning has occurred as shown by the difference between days; and that different groups did better on different days. The latter result, the interaction days × groups, was undoubtedly caused by the groups' doing better under hunger motivation than under thirst motivation in combination with the fact that hunger and thirst days did not coincide for all groups.

The analysis of variance gives no information as to the chief contributions to the between-groups variance, so *t* ratios were calculated to provide additional knowledge. These results show all but one of the between-groups differences to be significant beyond the .001 level. The exception is the difference between the 5- and 10-sec. delay groups, whose probability falls between .05 and .10.

TABLE 1

Breakdown of the Analysis of Variance

SOURCE OF VARIATION	*df*	MEAN SQUARE	*F*
Between groups	3	114.14	5.99**
Between *S*s in same group	36	19.06	
Total between *S*s	39	26.38	
Between days	99	24.92	8.67**
Days × groups	297	6.91	2.40**
Pooled *S*s × days	3564	2.87	
Total within *S*s	3960	3.73	
Total	3999		

** Signficant at the .01 level.

TABLE 2

Means and Standard Errors of the Delay Groups

GROUP	MEAN	*SE*	*N*
0	6.94	1.95	1100
5	6.66	1.90	1000
10	6.52	1.24	800
20	6.17	2.02	1100
Chance	5.00	1.58	1000

There is a possibility that the animals may have learned on the first trial which stimulus was positive that day. This necessitated an analysis of the responses made on the first trials of each day. It was found that the 0-, 5-, and 10-sec. delay groups did significantly better (at the .01 level) than the 20-sec. delay group. All groups achieved a level of learning significantly better than chance expectancy (at the .01 level).

A straight line was fitted to the mean number of correct trials per day presented in Table 2 by the formula $y = 1.90 - .037x$. This line reaches zero at about 52 sec.

DISCUSSION

As indicated by the data, the animals learned two separate responses to different sets of stimuli. The more important stimuli which enter into the stimulus patterns are:

S_{dh}	Internal stimuli associated with hunger deprivation
S_{dt}	Internal stimuli associated with thirst deprivation
W_l	White curtain on the left side
W_r	White curtain on the right side
B_l	Black curtain on the left side
B_r	Black curtain on the right side

The possible combinations of stimuli and their appropriate responses are:

S_{dh}	W_l	B_r	left-hand turn	eating
S_{dh}	W_r	B_l	right-hand turn	eating
S_{dt}	W_l	B_r	right-hand turn	drinking
S_{dt}	W_r	B_l	left-hand turn	drinking

This is clearly a discrimination of stimulus patterns with common components. Any suggestion that one pair of these stimuli alone could explain the results would be untenable. A discrimination between one pair of stimuli with each member consistently followed by the same response would only result in 50 per cent reinforcement.

Also, the possibility of differential secondary reinforcers is slight. Proprioceptive and intramaze stimuli are clearly ruled out since the correct response occurs equally often on each side. Also, the possibility of immediate secondary reinforcers following the response is greatly reduced by the use of frosted glass covering on the delay and goal boxes. The sensory experience of passing under each stimulus curtain is contiguous with other stimuli, which in turn are contiguous with the primary reinforcement. Through this process each curtain acquires secondary reinforcing power.

In the Grice experiment (4) only the experience of white in the stimulus alleys could be followed by reinforcement. These stimuli could have provided immediate secondary reinforcement, which they had acquired through the contiguity of their stimulus trace with the primary reinforcement.

In the present experiment, each stimulus curtain, having acquired secondary reinforcing power, would have equal reinforcing effect, regardless of response or the drive which was functioning. This has been shown in the studies of Estes (2, 3) and Meehl and MacCorquodale (9).

The method of equal opportunity was used in the Perin experiment (11) and in the present study. The mean level of learning reached by Perin's 10-sec. delay group was 82 per cent correct; by Mathers', 65 per cent.

In the Perin (11) experiment extinction intervened, thus preventing learning in the longer delay groups. In the 20-sec. delay group, three animals were extinguished, and in the 30-sec. delay group the number of extinctions was so great that the whole group was dropped.

It may seem strange that only one extinction occurred in the present experiment. The explanation lies in the difference in extinction criteria. Perin eliminated *S* if it failed to respond within 5 min. on three successive trials. In the present study, *S* was eliminated for failing to make a response within 30 min. on three consecutive trials. Although only one *S* approached this criterion, there were a few response latencies of 10 min. or more.

The present study indicates that it is possible for learning to occur under delay conditions in which only primary reinforcement can be found to be operating, and to a point beyond that revealed in the studies of Grice (4) and Perin (11). Since this discrepancy exists, there is need for a replication of the present study. This has to a degree already been done in the study by Heron (6) and in an unpublished study by Jean E. Carlin in the Minnesota laboratory. Both studies used a modification of the Yerkes-Watson light-dark discrimination box and methods very similar to those of the present study.

The mean percentage of correct responses per day computed from the learning curve in the Heron (6) study, based on 50 training periods, is approximately 68.4. This would correspond to the 69.4 per cent score for the zero delay group in the present study. The results of the Carlin study in terms of the mean percentage of correct responses per day, based on 684 trials, are as follows: for the zero delay group, 65; 5-sec. delay, 62; 10-sec. delay, 61; and 20-sec. delay, 62. It is believed that the comparability of these results with those of the present study is an indication of the reliability of the latter.

SUMMARY AND CONCLUSIONS

It is concluded that the gradient of reinforcement is not necessarily as short as indicated in previous experiments. Except for a delay of more than a very few seconds, reinforcement becomes so weak that almost unlimited learning opportunity is needed if significance is to be attained.

This experiment has shown that rats can learn significantly a problem which incorporates delays of primary reward up to 20 sec. This learning is manifested in the absence of differential secondary reinforcers.

The Spence (13) hypothesis would require of this experiment immediate differential secondary reinforcers in order for learning to occur. Since these conditions are not met and learning does occur, the Spence hypothesis is refuted and the Hullian position is upheld.

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PRACTICAL AND THEORETICAL SOLUTIONS TO DIFFICULTIES IN USING LICKLIDER'S RAT SHOCKER[1]

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Licklider (2) recently described a rat shocker based on the principle that two extended conducting surfaces in the neighborhood of each other form a capacitative circuit element. In constructing the apparatus, Licklider identified the surface of the rat in contact with a metal floor plate as one part of the condenser and the surfaces of two parallel metal plates perpendicular to the floor as the other part of the condenser.

Licklider's condenser principle of delivering a shock to an animal seemed ideal for shocking monkeys. Accordingly, we constructed a cubical cage having hardware-cloth sides and a sheet metal top and bottom. The top and bottom were viewed as forming one condenser plate and the sides as forming the other plate. The top and bottom were connected to the high voltage terminal of a Model-T spark coil; the sides, to the ground terminal.

We believed that the things that monkeys do to avoid shock in standard grids would not work in the cubical cage. There are no alternate grids to stand across; leaning against the sides would complete the circuit directly; crouching in the middle, climbing the sides, or bracing across a corner would complete the circuit through the monkey capacitatively. In short, the shock was to have been unavoidable.

But neither rat nor cat nor monkey received a shock unequivocally in the cubical cage. Because of lack of knowledge of lethal shocks using this system, a rat, a cat, and a monkey were tested in that order. All animals got shocked as they made direct electrical contact between the sides and the bottom or top. They sometimes got a shock as they moved about the floor, but they never got a shock when they remained motionless touching only the floor or sides.

ATTEMPTS TO MAKE LICKLIDER'S PRINCIPLE WORK

Such capriciousness made us think we had overgeneralized Licklider's principle, making the distance too great for the low energy capacity of the Model-T spark coil. One solution was to increase the shock intensity. This could be achieved by two obvious alterations in Licklider's scheme—alterations which were to provide greater capacity between the animal and the side plates as well as a higher-energy shocking circuit.

We constructed a higher-energy shocking circuit based upon the same principle as Licklider's. Both circuits use the principle of the familiar inductorium, except that the latter is not an autotransformer.

There are a few minor differences in circuit components between Licklider's and ours. We controlled shock intensity by varying the input voltage to a full-wave bridge rectifier which supplied direct current through an automobile radio vibrator-interrupter to a Mallory ignition coil. Licklider controlled shock intensity by varying a shunting spark gap. While the spark gap in Licklider's circuit might be expected to perform a voltage-limiting function as well as an oscillation-sustaining function through the negative resistance produced by the arc, a behavioral comparison of the two methods showed that the responses of rats to both shocks were the same; ours gained only in providing a better control and range of intensity.[3] Our use of an automobile radio vibrator interrupter produced a shock more uniform in amplitude and wave form than the Model-T circuit breaker.

The second method of increasing shock intensity involved changing the capacity between the animal and the side plates. We had to determine the limits within which Licklider's principle could be scaled up for animals larger than the rat. A model of Licklider's rat shocker was therefore constructed in order to determine the specific effect of side plate area and the distance between the animal and the side plates.

A Plexiglas box of the same dimensions as Licklider's was built. The bottom was left off so that the wire size and mesh of the floor could be varied; the metal side plates were not attached permanently so that their area and distance from the Plexiglas sides could be varied.

With a ¼-in. mesh floor and side plates 1¼ in. by 12½ in. (estimates from 2, Fig. 1) and with the higher energy shock we used, some animals could be shocked and some could not. The intensity or even the presence or absence of shock seemed to depend upon factors not under experimental control. When an animal got a shock, it was a good one, producing marked squealing, jumping, running, defecating, and urinating. An instant later it might be sitting still, washing its face, crouching, or sitting motionless, apparently receiving little if any shock.

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[1] This investigation was supported in part by a grant from Contract VAM23379 of the Veterans Administration.

[2] Beck and Waterhouse are responsible for the major portion of the investigation. Where individual responsibility can be assigned, Waterhouse made the critical observation that suggested the application of potential theory (observation 5). Runyon assisted in functionally specifying Licklider's capacity notion and in making the observations on human *S*s. He made the first observations on the dielectric electrode.

[3] The transients introduced by the spark gap and associated circuit elements are higher in frequency than .1 megacycle. These are well beyond the region of maximum sensitivity in human beings (1).

In an effort to prod one animal into activity we reached out to touch the rat after lifting aside the Plexiglas box. At the instant of contact Licklider's original spark-plug finding was confirmed for both rat and man. While the content of the human utterance may not have been identical to that of Licklider's *S*, we are confident that the meanings were similar.

Such unquestionable confirmation of Licklider's spark-plug experiment, replicated several times by accident by each of us, suggested that two effects might be operating: the relative distribution between the capacities to ground of the animal and the hot electrode, and a physiological effect depending upon the current density.

In the case of the first of these possible explanations, *E* and the animal would together form an electrical conductor of considerably larger capacity to ground than the animal alone. The second explanation of current density would mean that the charge concentration in *E*'s fingertip and the small region of contact with the rat would be increased. This charge-density notion regards *E* as a condenser plate whose size and surface irregularities provide conditions for both a large charge and a higher charge density. The latter would also be increased because the area of the rat's skin through which the current flowed when man and rat were shocked was much less than its skin area when only the animal was in the circuit.

These two notions were studied experimentally, but neither accounted for the inconsistency in shocking the animals. In an attempt to shock the animals consistently, we varied floor type and size, dielectric type and thickness, the area of the side plates and their separation from the animal, shock intensity and frequency. While the foregoing factors contributed to the shock when it occurred, they were not critical in determining its occurrence.

SOME CRITICAL OBSERVATIONS

The factors found to be critical are summarized below.

1. Animals which are insulated from ground get shocked just as they make contact with a *pulsed high-voltage electrode*.[4]
2. Animals which are insulated from ground get shocked just as they break contact with a pulsed high-voltage electrode.
3. Animals do *not* get shocked as they maintain contact with a pulsed high-voltage electrode.
4. Animals standing on a pulsed high-voltage electrode get shocked when they are touched with a *neutral electrode*.[4]
5. Animals get shocked as they stand on both a pulsed high-voltage electrode and a neutral electrode.
6. Animals standing on a *dielectric electrode*[4] get shocked as they touch a neutral electrode.
7. Animals suspended in mid-air above a pulsed high-voltage electrode get shocked when they are touched with a neutral electrode.

The next two observations are subordinated to the main qualitative findings because they do not determine the presence or absence of shock. They provide an empirical engineering principle for varying shock intensity in a set of new techniques for shocking described later.

The first of these constitutes a specification of Licklider's capacity notion. From studies of the current passing through anesthetized animals as a function of the area of the side plates and the distance between the animal and the side plates, it can be concluded that the capacity between the side plates and the animal is the sum of two capacities: one, the capacity between the animal and its electrical environment, and two, the capacity we controlled, which operates approximately as a parallel plate condenser.

The second principle for varying shock intensity states that the larger the neutral element, the greater the shock between the pulsed high-voltage electrode and the neutral element.

A final observation concerns the subjective nature of the shock received by a human being when he touched a dielectric electrode. The sensations from the shock can be described best at low-voltage inputs as a mildly vibratory, warm, humid feeling. As the voltage increases, this develops into a numbing sensation approaching the tingling feeling of having one's hand recover from going to sleep. For an instant, as one's hand rapidly approaches and quickly makes contact with the dielectric, it feels like an ordinary shock. At the highest possible voltages the shock can be felt even with the hand about an inch above the surface of the dielectric. This type of shock produces marked vasomotor activity, palmar sweating, blanching and reddening of the quick beneath the nails. It is not clear whether the sensory experiences associated with this shock are due to direct corona discharge through points on the skin or due to gradients developed within the skin. Possibly both are operating. The properties are worthy of further investigation.

THEORY

These observations immediately posed both an interesting and puzzling theoretical problem. What theory could rationalize the paradox of the observation that an animal can be shocked as it makes or breaks contact with a pulsed high-voltage electrode but not while *S* remains in contact with it? It will be seen that potential theory solves this problem. While an almost completely effective grid for shocking monkeys was discovered before the problem was solved theoretically, both its efficacy and the empirical observations depend upon the theory for understanding. It will further be seen that our early failures to confirm Licklider unequivocally and our success in developing still other techniques for shocking animals can be explained completely in terms of potential theory.

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[4] *Pulsed high-voltage electrode* refers to any conductor connected to the high-voltage output of the Mallory coil. Any conductor in the neighborhood of a pulsed high-voltage electrode but not in direct ohmic contact either with it or ground is called a *neutral electrode*. A sheet of insulating material such as Plexiglas placed on the surface of a plane pulsed high-voltage electrode is called a *dielectric electrode*.

Potential theory accounts for the set of observations. First, there is an electric field produced between the pulsed high-voltage electrode and ground. The field establishes a potential gradient. There are conductors including the animal itself. These conductors have a geometry of position, size, and shape. Further, these conductors are situated in dielectric media, namely, air and supporting insulating structures.

These four conditions are sufficient to produce voltage differences between the conductors. These voltages are determined by the field strength, the dielectric media, and the coefficients of capacity and induction determined by the arrangement, shape, and size of the conductors.

It is these voltages which can be used to shock animals; it is the presence or absence of these voltages in given empirical arrangements which determine the presence or absence of shock in the foregoing observations. The general principle depends upon analyzing the experimental conditions to see whether they can give rise to voltage differences. If these voltage differences exist, an animal can be shocked; if they do not, *S* cannot be shocked.

The first observation deserves particular consideration in terms of the theory. An animal, a conductor, approaching a pulsed high-voltage electrode increases its capacity with respect to that electrode. At the same time a local potential is induced in *S* as a conductor. If the potential difference between *S* and the high-voltage electrode is sufficient to ionize the air, the charge will be transferred from the high-voltage electrode to *S*. This transfer will produce the momentary high current which shocks the animal. After the charge is transferred, the animal and the electrode will be equipotential, and no shock can ensue.

The peculiarities in the operation of our model of Licklider's rat shocker can now be understood. It shocks a rat largely because of an initial fortuitous contact an animal might make with the dielectric electrode on the sides of the box. If *S* gets such an initial shock, it might jump off the floor. If it jumps, it gets one shock as it leaves the floor and another as it lands. These shocks bounce the animal here and there within the narrow confines of the box, shocking and reshocking it. Some animals learn to remain still, thus avoiding the shock because they are at the same potential as the floor. The presence or absence of shock is therefore not under complete experimental control in the Licklider arrangement; the shock depends upon the vagaries of an animal's responsiveness and learning. The width of Licklider's shocking alley is critical for making his system work. He believed capacity between the animal and the side plate was critical. We believe that the animal is shocked because it touches the dielectric electrode. If Licklider's notion were correct, then an animal once shocked should continue being shocked. That it does *not* continue to be shocked has been our finding. This finding is contrary to the capacity notion.

SOME CONFIRMING OBSERVATIONS

If our integration of the facts in terms of potential theory be correct, Licklider's rat shocker should not work when scaled up to human size. Contradictory to the prediction from Licklider's theory, we predicted that a human *S* standing barefooted on a pulsed high-voltage electrode, near a vertical grounded metal plate, would not receive a shock. Three *S*s received no shock whatsoever under those conditions. These same subjects reported only the vibratory feeling when they touched a ⅜-in. thick Plexiglas sheet covering part of the vertical metal plate. The voltages used were sufficient to produce a 3-cm. spark between a plane surface and the tip of a piece of no. 20 wire. The failure of *S*s to experience shock in this situation is not due to lower innervation of foot than hand. The shock does not occur when one hand is in firm contact with a pulsed high-voltage electrode. If pressure is not maintained, shock is experienced. This is believed to be due both to contact variation produced by tremor and to local variations in current density.

The latter current density variation constitutes the only situation where pure capacitative effects can be demonstrated. In order to isolate this effect experimentally, controlling for the effects of stray capacity, two rods differing in size were connected to one another and to a pulsed high-voltage electrode. When a human *S* held his finger continuously on the end of the ⅜-in. diameter rod, he could not feel a near-threshold shock unless he touched another neutral electrode. When he held his finger on a 1/16-in. diameter rod he was unable to reduce the shock below threshold even though he pressed as hard as he could. This is the only instance of direct application of Licklider's notion. It can be expected to operate only when current density can be made sufficiently high by using minimal contact areas. Indeed, even the spark-plug shock would be expected to disappear if, after the shock of initial contact, *S* held the spark plug with enough grip area to avoid current density effects.

A NEW SHOCKER

Aside from understanding the original observations and the irregularities in the Licklider system, the theory and principles are useful in the development of techniques for solving our original problem, shocking a monkey. The range of possibilities is limitless, but all that is necessary is to arrange the conductors in the shocking cage such that an animal is always in contact with two pieces of metal which differ in potential. One particular solution we have effected consists in connecting the alternate odd-numbered bars of a grid to each other and to a pulsed high-voltage electrode. The even-numbered bars of the grid are left electrically isolated from each other. The sides and back of the cage are made of smooth metal and are insulated from both sets of grid bars. The front of the cage is made of glass for observation purposes.

This monkey shocker is very effective. The smooth sides afford little purchase to a monkey's modes of gripping. If it stands between any odd and even bar, *S* will get a shock. If it leans against the side of the cage while standing on an odd bar, *S* will get a shock. If it leans against the side while standing on an even neutral bar, *S* may get a shock if the potential gradient between those two neutral elements is sufficiently steep. If it is not, it is a simple matter to make and break contact between the odd bars and the sides of the cage. If the animal defecates, the shock does not disappear from the entire grid but just from the three adjacent grid elements made equipotential by a bolus shorting a juxtaposed pair. This nonshorting feature holds only when the even elements are insulated from each other. That is, the grid has a uniform potential if an interconnected set of neutral elements is connected to the pulsed high-voltage electrode set by a bolus.

There are three ways of increasing the intensity of the shock: voltage, area of a neutral element, and the gradient. The latter is increased either by connecting the neutral elements to ground through separate condensers or by rearranging the position and size of the elements with regard to each other and the pulsed high-voltage electrode.

SUMMARY

Potential theory encompasses a new set of observations growing out of a study of difficulties encountered in using Licklider's rat shocker. The theory explains these difficulties, gives meaning to the observations, and provides new techniques for solving many of the problems encountered in shocking animals. In the course of the study a promising new shock stimulus using dielectric electrodes was discovered. Finally a specific practical solution to the problem of shocking monkeys is presented, an electric field shocker.

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TASTE AND POST-INGESTION FACTORS IN SPECIFIC-HUNGER BEHAVIOR[1]

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Animals are capable of regulating their eating and drinking behavior so as to supply themselves with larger than normal amounts of substances in which they are deficient (e.g., see 14, 15, 16). This kind of control system has also been demonstrated in humans (15). These are the classical observations in the area of specific hungers, and they stimulated the interest of workers in many different fields. Biochemists, physiologists, nutritionists, and psychologists alike have spent considerable time over the past 20 years trying to understand just how such a control system could operate.

Psychologists in particular find the behavior interesting because it represents a case of motivated behavior with fairly clear-cut physiological correlates. It could be hoped that the field of specific hungers might supply a chance to specify rather exactly the physiological basis of an interesting pattern of behavior.

Since the original observations of Richter (14), workers in this field have broadened considerably the range of phenomena that are considered examples of specific-hunger behavior. For example, normal rats prefer certain concentrations of salt water and sugar water to plain water (1, 17). Such specific preferences have been demonstrated with many other substances as well (e.g., 18). Further, for some particular types of solution, such as, for example, sugar water, the rat has a strict hierarchy of preference for different concentrations of the solution (17). In short, when a normal rat is given access to particular concentrations of many solutions, it will ingest fairly specific amounts of them. The problem is to find out what factors determine the volume that the animal will ingest.

Although "learning" has been shown capable of playing a role in some cases of preference behavior (23), the present attempt has been to keep chances for learning at a minimum and pay particular attention to the physiological factors underlying the behavior.

Two general physiological possibilities suggest themselves. First, food preferences could be based simply on *taste factors*. Workers have produced evidence for and against this notion (7, 12, 15).[3] Following taste, so to speak, specific volumes of particular solutions might be taken because of effects they have after they are swallowed—so-called *post-ingestion factors* (19). Solutions, of course, have both chemical-specific and colligative characteristics, and either set of characteristics could turn out to be critical after ingestion.

EXPERIMENT 1: PREFERENCE FOR GLUCOSE AND FRUCTOSE SOLUTIONS

Aside from obtaining normative data for the following experiments, there is one important reason for being interested in the relative preference of the rat for different solutions of fructose and glucose. Fructose has considerably more sweetening power than glucose. According to psychophysical data on humans, fructose is roughly twice as sweet as glucose (3). If taste—specifically sweetness—is an important determiner of how much of a solution the animal will drink, one might expect some interesting differences between the intake curves for these two carbohydrates.

Method

In all the various experiments in this paper, the rat's sugar preference is measured by the single-bottle method. In the single-bottle situation, the animal is on a water-deprivation schedule and receives a different concentration of sugar solution in its test bottle for 1 hr. on successive days. With this procedure, the measure of the animal's preference among the different concentrations of sugar is the *volume* of the particular solution that the animal drinks during the test hour.

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[1] The experiments reported in this paper were performed in partial fulfillment of the requirements for the degree of Doctor of Philosophy at The Johns Hopkins University.

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[3] Carr, W. J. Personal communication.

For all the present research, the animals were on a 16-hr. water-deprivation schedule, and food was available ad libitum except during the test hour. The precise schedule is shown in Table 1.

Since the animal is thirsty in the single-bottle situation and has only 1 hr. to drink from a single bottle, all the drinking behavior occurs in a short time. This fact gives the single-bottle method two important advantages: (*a*) The drinking can be influenced by physiological variables of a transitory nature and (*b*) the rate of drinking can be conveniently measured over such a short interval. The minute-to-minute drinking rate of the animals was obtained by using a continuously recording, electronic drinkometer which has previously been described (8).

The animals in this first experiment were tested in the single-bottle situation on concentrations ranging from .1 per cent to 40 per cent for both glucose and fructose. The glucose and fructose series were run in turn. A preliminary study had shown that the intake for a particular solution did not change in any systematic way with repeated daily observations, so for the two carbohydrates in this first experiment a single ascending-descending presentation was used. In this way, each animal was checked twice for each concentration of each sugar. The animals were given water for their test solution on several occasions before, during, and after the sugar series, to afford a base line for the sugar intakes.

TABLE 1

Experimental Schedule

9:00 A.M. to 10:00 A.M.	Test period. Animals given 1 hr. to drink one of the experimental solutions. No food in cage.
10:00 A.M. to 12:00 M.	No food or fluid available in cage.
12:00 M. to 5:00 P.M.	Food and water available ad libitum.
5:00 P.M. to 9:00 A.M.	No fluids available. Food ad libitum. (16-hr. water deprivation)

Animals, cages, and illumination. Brown and hooded rats, descendants of the Lashley strain, were used throughout the entire research. At the start of this first experiment, the eight animals were three months old. The test drinking was always done in the animals' own home cages. The cages were always kept under controlled illumination so that there were 12 hr. of light and 12 hr. of dark each day. The test drinking always took place 3 hr. after the start of the light cycle.

Diet and test solutions. The rats were fed Purina Laboratory Chow, either checkers or meal. The glucose and fructose were of reagent grade, and the stock solutions of sugar were handled with precautions to avoid contamination with fungi and bacteria. Fresh experimental solutions were made each day from these sterile stock solutions.

Results

The main results of Experiment 1 are shown in Figure 1. The concentrations have been put on a log scale simply for graphic clarity because the intakes change so rapidly over the lower concentrations.

Despite the greater sweetening power of fructose, it was maximally preferred at the same concentration as glucose. Further, across the range of concentrations in which the carbohydrates are preferred significantly over water, there is no concentration at which more fructose than glucose is ingested. At the −1.0 and −.5 log concentration points, where the mean fructose intakes exceed those for glucose, the intakes do not differ significantly either between the two carbohydrates or between carbohydrate and water. To the extent that one is willing to assume that fructose is also sweeter for the rat, these data do not support a simple notion about the role of taste in the specific hunger for sugar.

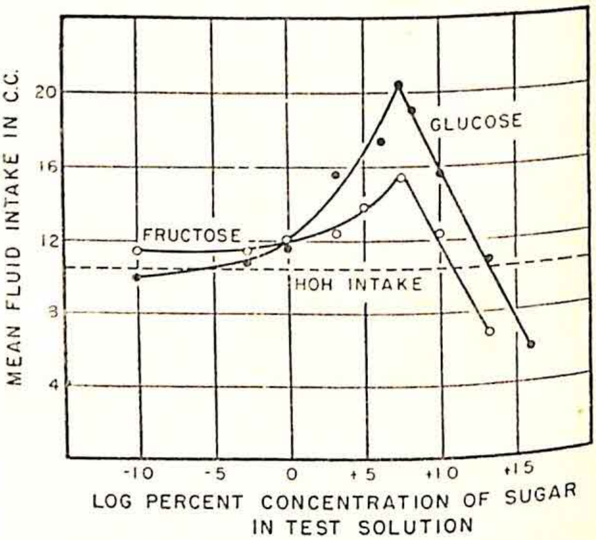

FIG. 1. Intake during test hour of various concentrations of glucose and fructose. Each point is the average of two separate readings taken on each of eight animals.

For fructose the aversion point (concentration at which water becomes more preferred than sugar solution) is lower than in the case of glucose. This one point might be taken as suggesting that taste is playing a role in the declining limb of the preference function, since fructose might be expected to get too sweet at a lower concentration than glucose.

There is one final fact that is apparent in Figure 1. It turns out to be of considerable interest with regard to some later findings. The peak preference point for both glucose and fructose is for the 5.3 per cent solutions. This concentration is approximately isotonic with the body fluids of the animal for both of the carbohydrates under consideration.

Some rate curves for the drinking of a few sample solutions are shown in Figure 2. Their shape tells some interesting things about the time course of the drinking behavior. In the first place, for all the concentrations the animals start drinking at their maximal rate. Since they are thirsty at the start of the test, this is not too surprising. Further, the animal maintains this rate of drinking until it has ingested about as much of the particular solution as it will take for the test hour. After this original burst of drinking, the animal only comes back for an occasional sip during the rest of the test period.

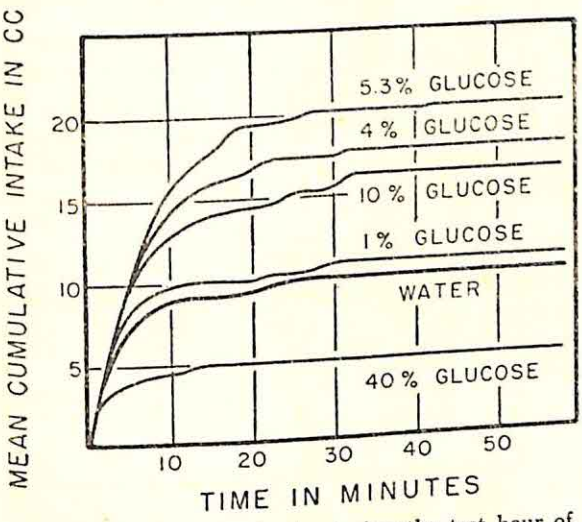

FIG. 2. Cumulative intake during the test hour of various concentrations of glucose and water. Each of the curves is the average of the cumulative intakes of eight animals.

This is to say, within 5 min., and shorter for some of the less-preferred solutions, the animal has already committed itself to taking some particular volume of the solution. Whatever mechanism is operating to halt the animal's further drinking, it can operate in a very short time after the start of the drinking behavior. Despite the absence as yet of more direct evidence for a role for taste, it must be noted that taste would be capable of monitoring such a rapid "decision" on the part of the animal.

EXPERIMENT 2: STOMACH LOADING OF GLUCOSE SOLUTIONS

The first point to be settled when one considers the problem of post-ingestion effects is simply whether an ingested solution can operate to affect further ingestion. For example, does 40 per cent glucose, after it has been ingested, act in such a way that, when an appropriate volume has been drunk, it inhibits the further drinking of 40 per cent glucose? This kind of control system could be considered a "negative feedback" system.

The most direct approach to this problem seemed to be to use a stomach-tubing technique and load variously preferred solutions of glucose into the animals' stomachs and observe the effect of these "loads" on their later drinking of glucose.

Method

The stomach loading of these glucose solutions was handled as follows: while one person held the rat with the upper teeth hooked over a fixed wire loop and pulled the lower jaw open with a second loop placed over the lower teeth, E passed a blunt-ended rubber tube down the animal's esophagus and into its stomach. A good stomach tube turned out to be a French No. 8 Robinson-type rubber catheter. It is best to have the catheter well lubricated with mineral oil, and it is helpful to have a hanging drop of oil on the tip of the catheter to initiate a swallowing reflex at the time the catheter is introduced into the esophagus. When the catheter has been passed several inches, 3 cc. of the loading solution is put into the stomach with a calibrated syringe attached to the end of the catheter.

Three cubic centimeters of three different concentrations of glucose were used as stomach loads (5.3, 20, and 40 per cent glucose). The animals were allowed on successive days to drink four different test solutions (water, 2 per cent glucose, 5.3 per cent glucose, and 20 per cent glucose). The same eight rats were used as in the previous experiment. These 12 conditions and eight rats were run in a factorial design, using the single-bottle method as described above. The animals were allowed access to the test solutions for drinking 15 min. after the stomach load was introduced by tube.

Results

The mean data are shown in Figure 3. Increasing concentrations of the glucose load have systematic effects on the amounts of the different test solutions that the animals will later drink. In the case of all the test solutions, except the unchanging 2 per cent solution, the differences between the intakes with the 5.3 per cent and 40 per cent loads are all significant between the .01 and .03 levels of confidence. The intakes following the 20 per cent load all fall systematically into the consistent trend, but the intermediate differences (5.3 per cent load vs. 20 per cent load and 20 per cent load vs. 40 per cent load) are only in one case significant at the .05 level of confidence.

This figure, which summarizes all the data from this experiment, shows two main effects: (*a*) As the concentration of the sugar load increases, the animals' intake of water during the test period also increases. (*b*) The intake of the two more concentrated test solutions (5.3 per cent and 20 per cent glucose) bears a reciprocal relation to the water intake—they decrease as the stomach load becomes more concentrated. The 2 per cent glucose solution occupies a sort of compromise position, and its ingestion is relatively unaffected by the stomach loads.

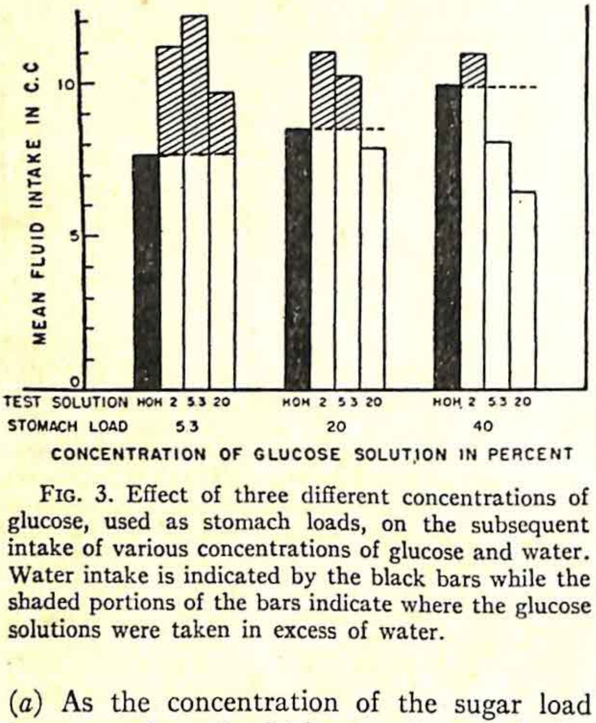

FIG. 3. Effect of three different concentrations of glucose, used as stomach loads, on the subsequent intake of various concentrations of glucose and water. Water intake is indicated by the black bars while the shaded portions of the bars indicate where the glucose solutions were taken in excess of water.

The simple point here is that it is possible for glucose solutions that have by-passed the taste receptors of the animal (i.e., have been loaded by tube) to have a differential effect on the subsequent intake of other glucose solutions. Further, the less preferred the concentration is as a test solution (40 per cent < 20 per cent < 5.3 per cent), the more effective it is as a depressant when used as a stomach load. These findings clearly suggest the existence of a post-ingestion factor that might operate in specific-hunger behavior.

EXPERIMENT 3: STOMACH LOADING OF FRUCTOSE SOLUTIONS

This systematic effect of different glucose loads raises an interesting question about fructose. Since, concentration for concentration, fructose solutions are less preferred than glucose solutions over the range where either are preferred significantly over water (see Fig. 1), the question arises: Can this lower preference for fructose also be due to some sort of post-ingestion factor? The present experiment supplies some information on this point.

Method

Three cubic centimeters of both 5.3 per cent glucose and fructose were used as stomach loads and, in a factorial design, the eight animals were allowed to drink 5.3 per cent glucose, 5.3 per cent fructose, and water.

Results

Although the effect was not a large one, the main finding here was that the fructose load did indeed depress both glucose and fructose drinking more than did the glucose load. Since the difference in preference for 5.3 per cent fructose and 5.3 per cent glucose was small—only about 5 cc.—the small magnitude of this present effect is probably not surprising. When all the cases of fructose loading and sugar drinking were averaged and compared with the average effect of the glucose loading, the results showed that six of the eight rats drank less sugar solution when they had been loaded with fructose. The mean difference was 1.06 cc. (single-tailed $p = .03$). The fructose load also produced a greater water intake than did the glucose load, but the difference was not significant.

It is interesting that the effect on sugar drinking is in line with the previous stomach-load data. Again, the less-preferred solution in the single-bottle situation (in this case, fructose) had the more depressant effect when used as a stomach load.

EXPERIMENT 4: TIME COURSE OF THE POST-INGESTION EFFECT

Although the above experiments show the existence of a post-ingestion factor, it remains to be seen whether such an effect could take place rapidly enough to be able to play a controlling role when the animal is actually drinking the solutions rather than having them artificially loaded into its stomach by tube. In Experiments 2 and 3, the animals had a 15-min. delay between the stomach loading and the drinking of the test solutions, but if the post-ingestion factor normally plays a part in controlling an animal's fluid intake, it would have to operate much more rapidly than that. This present experiment set out to discover how rapidly this effect could operate.

Method

Two different procedures were used, but they rendered similar results and are reported here together.

First, using only one of the test solutions from the previous experiment (5.3 per cent glucose), the same eight animals were stomach loaded with the same three concentrations but were given *immediate* access to their drinking bottles. There was only about a 15- to 30-sec. delay between the loading and the drinking.

The second technique allowed the rats to self-load themselves. An experimental arrangement was designed that allowed the animal to start the hour of drinking by first ingesting 3 cc. of an appetizer solution from a small glass tube and then, with a maximum 15-sec. delay, switch to the usual bottle for the main test solution of the day. This technique adds a taste factor to the stomach load that the animal receives and, furthermore, affords a control for the influence of the stomach-tube procedure. The same concentrations of glucose that were used as the loads above were also used here as the appetizers. The test solution was again 5.3 per cent glucose.

Results

The mean results of both the immediate tube-load and the self-load procedures are presented in Figure 4. For sake of comparison, the 5.3 per cent test-solution data from the 15-min. delay experiment (Experiment 2) are indicated as a dotted line. The most important point to notice is that even when there is only a matter of seconds between the stomach load and the drinking, the volume intake of 5.3 per cent glucose is affected in the same direction as in the 15-min. delay case reported above. Namely, the more concentrated the stomach load or the appetizer, the more it depresses the intake of 5.3 per cent test solution. The extremes with both techniques (i.e., 5.3 per cent load or appetizer vs. 40 per cent load or appetizer) are significantly different below the .01 level of confidence.

These present results, when considered together with the data on rate of drinking shown in Figure 2, give a clear picture of the speed with which this post-ingestion effect can operate. In the extreme case of the 40 per cent tube load, the animals take an average of about 6 cc. of the 5.3 per cent test solution. Since, on the average, rats under the present circumstances drink a little more than a cubic centimeter per minute, this means that the 40 per cent tube load has had its effect on the animals' drinking in a little under 6 min. It seems reasonable that this is rapid enough for the effect to be a feasible controlling mechanism in the drinking behavior of the animal.

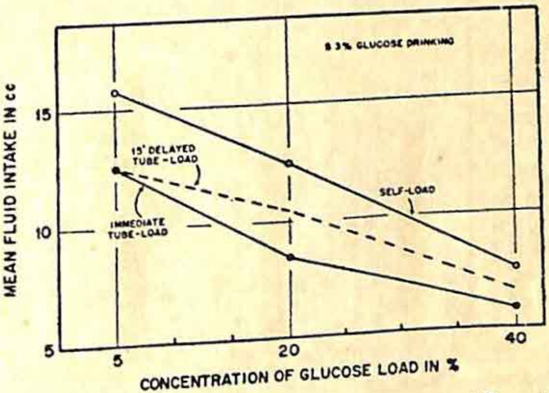

FIG. 4. Comparison of the effect of three different concentrations of glucose when used as a delayed load, immediate load, and self-load (see text). Curves show intake during subsequent test hour of 5.3 per cent glucose solution.

The differences between the slopes of the three functions shown in Figure 4 are not significant with the number of observations available in the present study. A more extensive experimental attempt to evaluate these differences, however, might show that the depressing effect of the stronger loads has, in fact, started to fade after the 15-min. delay. The fact that the self-loading data are higher over all is explained by the fact that the trauma of the tubing procedure routinely depresses later drinking by several cubic centimeters.

EXPERIMENT 5: STOMACH LOADING OF SACCHARINE SOLUTIONS

Because of the striking effects obtained from stomach-loading glucose and fructose solutions prior to drinking various test solutions, it was felt of interest to look into the generality of this effect.

Saccharine loads were chosen as instructive since saccharine solutions are ordinarily considered to taste somewhat like carbohydrates, and yet, of course, they are preferred by humans and rats alike at much lower concentrations than carbohydrates.

Method

The same eight animals were offered various concentrations of saccharine, employing the same drinking situation and schedule described in the previous experiments. These preliminary data yielded a preference for saccharine of roughly the same type as in Figure 1 for glucose. The concentrations for saccharine were over a much lower range, of course, and were well in line with previous reports of rats' preference for saccharine solutions.

From these preliminary data, three concentrations of saccharine were chosen for use as stomach loads in the main experiment. In keeping with the results of the other stomach-loading experiments reported above, these three concentrations were: (*a*) the peak preference concentration (.25 per cent), (*b*) a concentration chosen from about midway on the declining limb of the preference function (.5 per cent), and (*c*) a concentration from the tail of the declining limb of the preference function (1 per cent). For these three concentrations of saccharine, respectively, the mean intakes in the pilot study were 14.2 cc., 8 cc., and 4 cc. during the hour test period.

For the present experiment, the eight animals were loaded every other day with one of the three different concentrations of saccharine. The lower concentrations of saccharine were loaded first to minimize any cumulative effects of the saccharine administration. The animals were always given access to their test solution immediately after the saccharine solution had been loaded into their stomachs. The test solution for drinking during the test hour was always 5.3 per cent glucose solution. This concentration of glucose was used as the test solution because of the previous data on stomach tubing already available.

Results

The results were quite clearly negative from the standpoint of any post-ingestion effects of the loaded saccharine. In fact, to an insignificant extent, the results were the reverse of what might have been expected.

The mean data are shown in Table 2. From a statistical viewpoint the three different saccharine loads did not have any different effect on the ingestion of the glucose test solution. Despite the fact that the three saccharine loads were preferred by the animals in a clearly diminishing order (i.e., .25 per cent > .50 per cent > 1.0 per cent), they had no parallel effect on later drinking of the glucose test solution when they were used as stomach loads.

This negative finding seems striking when one recalls how easy it is to demonstrate post-ingestion effects by this stomach-loading technique—when such effects are present. The author feels that these present negative data strongly suggest that the case of *saccharine* preference could well be controlled primarily by taste.

TABLE 2

Effect of Saccharine Stomach Load on the Drinking of 5.3 Per Cent Glucose Solution

CONCENTRATION OF SACCHARINE SOLUTION USED AS LOAD	MEAN VOLUME (IN CC.) OF 5.3 PER CENT GLUCOSE INGESTED DURING HOUR FOLLOWING THE LOADING
.25%	12
.50%	12.9
1.0%	13.4

EXPERIMENT 6: COMPARISON OF THE EFFECT OF GLUCOSE, NaCl, AND UREA SOLUTIONS WHEN USED AS STOMACH LOADS

Consideration of the intestinal absorption rate of glucose from solutions of various concentrations (2, 4, 10, 13, 22) suggested that the post-ingestion mechanism demonstrated above with glucose could not depend on the amount of glucose absorbed into the internal environment of the organism. On the other hand, it is possible to think of several ways in which the stomach-loaded solutions could have their effect while still in the stomach. The speed with which the effects take place indirectly supports the notion that something critical might be taking place in the stomach. To narrow down the possible mechanisms, it seemed pertinent to establish first whether it is the chemical specific or colligative properties of the stomach-loaded solutions that are crucial for the effect of the loads on later drinking. For this purpose the present experiment was designed, employing solutions of three different compounds which were matched in terms of their colligative properties.

Method

Three different concentrations of urea and NaCl solutions were used as stomach loads. The concentrations were chosen to be approximately isosmotic with the 5.3, 20, and 40 per cent glucose loads previously employed. The osmotic pressures were calculated on the basis of the freezing-point depression produced by the various concentrations. Allowance was not made for the small extent to which urea and glucose are not perfect nonelectrolytes. For urea the three concentrations were 1.7, 7, and 14 per cent; for NaCl, .9, 4, and 8 per cent. Three cubic centimeters of the load to be used for the day were introduced into the stomach of the animal by tube 15 min. prior to the time at which the test solution was made available to it. The daily order in which the different stomach loads were used was varied from animal to animal to control for possible sequence effects. Six animals were used for the salt loads, and a second group of eight animals was used for the urea loads.

Results

The results, presented in Figure 5, are clear-cut. The urea and NaCl data are from this present experiment, and the data resulting from glucose load are replotted from Experiment 2 for the sake of comparison. It can be seen that both urea and NaCl loads, when matched osmotically with the glucose loads, have the same relative effect on subsequent intake of glucose solution as the glucose loads themselves. The reader is reminded that the three different loads were used on three different groups of animal so that no significance can be attached to the over-all difference in level of intake for the three loads. Only the slope of the three functions is pertinent to the present point. The difference between the two extreme NaCl loads yields a *t* that is significant beyond the .01 level of confidence with 5 *df*, using a single-tail test. The same comparison with the urea load with 7 *df* is significant at the .03 level of confidence. Intermediate differences are not significant but fall in the correct direction according to the original hypothesis.

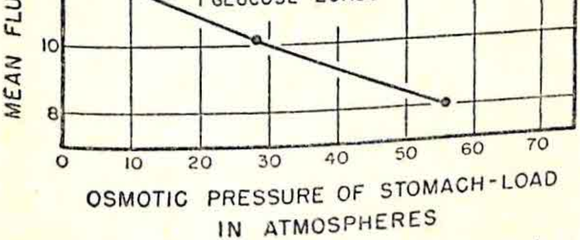

FIG. 5. Effect of three different solutions, used as stomach loads, on the subsequent intake of 5.3 per cent glucose solution. The three different concentrations used for each load were approximately matched between loads in terms of osmotic pressure (see text).

This parallel between glucose, urea, and NaCl becomes even more striking when one realizes that all the loads produce a comparable increase in water intake. This was shown above for glucose. For urea, the 14 per cent load increased water intake in the subsequent test period by 5 cc. more than the 1.7 per cent load. This difference yielded a *t* that with 7 *df* was significant well beyond the .01 level even with a two-tail test. Other workers have shown that NaCl loads have comparable effects on later water intake (20).

EXPERIMENT 7: INTRAPERITONEAL LOADING OF GLUCOSE SOLUTIONS

The positive results obtained in the experiment just reported indicated clearly that the water and electrolyte balance of the animal is capable of influencing its preference behavior. To pursue this idea further, a series of intraperitoneal glucose loads was worked out that produced an increase in water intake that was roughly comparable to what the various stomach loads produced.

Method

Six rats were placed on the same 16-hr. water-deprivation schedule described above. One hour prior to the test period, 5 cc. of a glucose solution were introduced into the peritoneal cavity through the abdominal wall with a No. 20 hypodermic needle and syringe. This intraperitoneal load was either 5.3, 10, or 20 per cent glucose. The solution for drinking during the test period was either water or 5.3 per cent glucose. These three loads, two test solutions, and six animals were combined in a factorial design.

Results

The results are at variance with what might have been expected from the way in which glucose loads behave when introduced into the stomach. As shown in Figure 6, the water intake was indeed increased. The difference between water intake with the 5.3 and 20 per cent loads, using a single-tail test, yielded a *t* that was significant at better than the .01 level of confidence with 5 *df*. Despite this increase in water intake, however, the intake of 5.3 per cent glucose was neither systematically nor appreciably influenced.

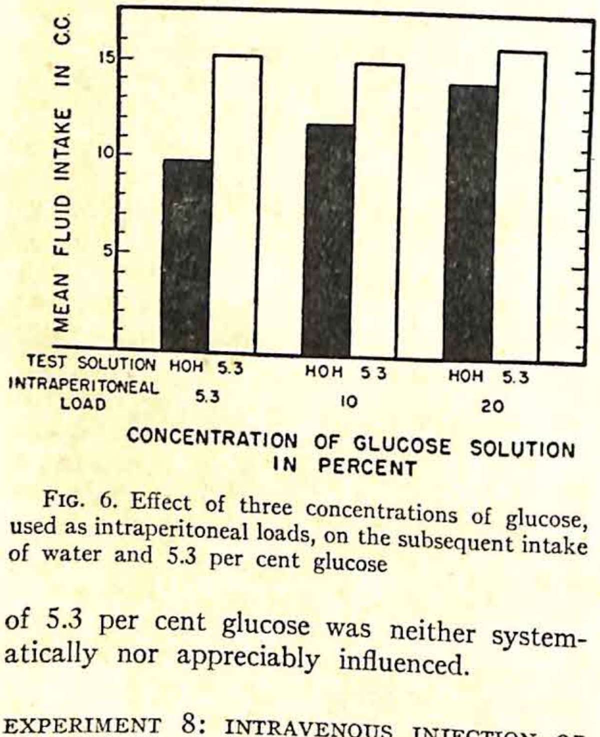

FIG. 6. Effect of three concentrations of glucose, used as intraperitoneal loads, on the subsequent intake of water and 5.3 per cent glucose

EXPERIMENT 8: INTRAVENOUS INJECTION OF NaCl SOLUTION

Although both stomach and intraperitoneal loads of appropriate concentrations of glucose produced an increase in the intake of water, only the stomach load resulted in a comparable decrease in the intake of 5.3 per cent glucose. This discrepancy raises the question of whether the stomach is a necessary link in the differential effect of glucose loads on the ingestion of water and glucose solution. Since intravenous injection of NaCl solution will produce thirst without directly involving the stomach, it was hoped that this procedure would supply some definitive information.

Method

Although an intravenous technique involving the superficial vein on the posterolateral aspect of the thigh of the rat was developed, the vein would not remain patent for more than a single NaCl injection. Thus, only two experimental observations could be made on each rat—an insufficient number for present experimental purposes. For this reason it was decided to employ the rabbit because of its easily accessible and abundant ear veins.

The rabbit that was employed weighed 2,900 gm. It was placed on the identical 16-hr. water-deprivation schedule as described previously for the rat. During the test period it was placed in a standard rabbit box and an inverted 500-cc. graduated cylinder supported by clamps on a ring stand was placed in front of the box so that the ¼-in. glass tube extending from the cylinder was available to it.

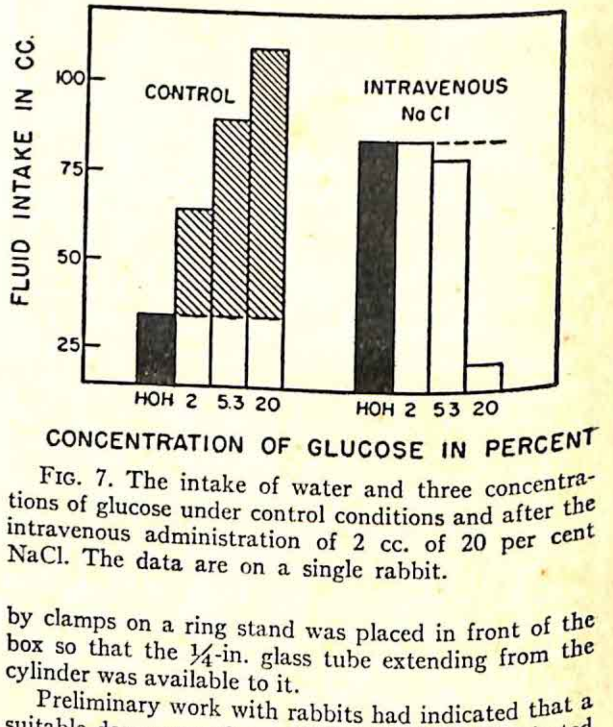

FIG. 7. The intake of water and three concentrations of glucose under control conditions and after the intravenous administration of 2 cc. of 20 per cent NaCl. The data are on a single rabbit.

Preliminary work with rabbits had indicated that a suitable dosage was 2 cc. of 20 per cent NaCl injected slowly over about a 30-sec. period. At the end of the usual hour's test period, however, the effect of this injection was starting to wear off. For this reason, the procedure of allowing only a 15-min. drinking period for both control and experimental days was adopted for the experimental animal. On control days the animal was held down on a table in the usual way and the ear was stuck with a hypodermic needle, but no intravenous injection was made. Immediately following either the control or intravenous procedure the animal was placed in the box and the test solution for the day made available to it. The test solution was either 2, 5.3, or 20 per cent glucose or water. The control and experimental procedures were used on alternate days. Each test solution was used twice under both control and intravenous conditions.

Results

The results are shown in Figure 7. The similarity between these data and the data resulting from the stomach loading of hypertonic glucose solutions, as reported above, is very striking. Following the injection of intravenous NaCl, the water intake increased, as would be expected, and likewise the intake of the hypotonic 2 per cent glucose solution increased to a lesser extent. For the more concentrated solutions of glucose, however, the opposite was true. Both absolutely and relative to the water base line, the intake of 5.3 and 20 per cent glucose solution was diminished. This is precisely the form of the previous data which resulted from the stomach loading of the hypertonic, less-preferred glucose solutions.

DISCUSSION

This present study bears specifically on the mechanism mediating the declining preference for the higher concentrations of carbohydrate solutions. Experiments 2 and 3 suggest that the higher concentrations (stronger than 5.3 per cent) are ingested in smaller volume (i.e., are less "preferred") because of their effect after ingestion. Experiment 6 shows that part or all of this post-ingestion effect is dependent on the concentration of the stomach load regardless of the specific compound involved. In the case of glucose, NaCl, and urea, the two more concentrated, hypertonic loads depressed the later ingestion of 5.3 per cent glucose as compared with the amount ingested following the less concentrated, isotonic load (i.e., 5.3 per cent glucose, .9 per cent NaCl, or 1.7 per cent urea). The inquiry, then, narrows down to the chain of events that follows the arrival in the stomach of any hypertonic solution.

One thing that happens in the stomach is a fairly rapid withdrawal of fluid (10, 13). Before such hypertonic solutions are passed on to the small intestine, they are diluted to a concentration approximating isotonicity (11). This fluid withdrawal has two things to recommend it as the crucial factor for the post-ingestion or stomach-loading effect. First, it is an effect that is quite nonspecific to the type of solute, depending primarily on the degree of hypertonicity of the solution. Secondly, this process in the stomach occurs immediately after ingestion, which satisfies the time requirements as delineated in Experiment 4.

The fluid withdrawn into the stomach is hypotonic (11). Thus, the animal not only loses fluid into the lumen of its stomach but also is left for a period of time in a relatively hypertonic condition. This hypertonicity is probably the basis for the increased thirst which was uniformly one of the effects of the various hypertonic stomach loads.

It is suggested that this transitory hypertonic or dehydrated state is the physiological mechanism that operates to limit further ingestion of the hypertonic solution that had set off the chain of events here postulated. Before inquiring further into what the details of such a mechanism might be, let us examine Experiments 7 and 8 with this notion in mind.

The intraperitoneal glucose did indeed produce increased thirst, but it did not produce a depression of glucose drinking. Superficially, this appears to be a negative bit of evidence for the dehydration mechanism that has just been proposed. A closer look at the effects of intraperitoneal glucose, however, suggests an interesting reason why this method of producing thirst might not have any influence on the drinking of glucose solutions. Fluid withdrawn into the peritoneal cavity by injected glucose carries with it considerable solute (5, 9). Thus, although the internal environment of the animal is deprived of fluid by this procedure, the animal may not be rendered hypertonic. This would presumedly be a case of production of thirst by decreased plasma volume (9). Pending actual comparison of these two kinds of fluid loss under experimental conditions comparable to the present ones, the most that can be clearly stated here is that at least there are two kinds of thirst—thirst that is accompanied by a decreased preference for 5.3 per cent glucose solution and thirst that is not. This point is of interest in view of the debate on whether decreased plasma volume or hemoconcentration is, in the usual case, the adequate stimulus for thirst (9). The suggestion here seems to be that when hypertonicity is involved in the production of the thirst (the stomach-load case), then one also sees a depression in the intake of the appropriate glucose solutions. When the thirst is not associated with hypertonicity (as suggested for the intraperitoneal glucose case), then the glucose drinking is not depressed.

The use of intravenous NaCl is one way to check on the idea that hypertonicity is responsible for the effect of the various stomach loads on glucose intake. It is clearly a case in which the increased thirst is the result of hypertonicity in the internal environment of the organism (6). It is confirmatory of the present hypothesis, therefore, that after intravenous NaCl the rabbit's preference for the stronger glucose solutions did indeed diminish in the expected way.

In speaking of the organism as "hypertonic," the implicit reference has been to the extracellular fluids. In actual fact, of course, if the chain of events stopped at that point, it would be difficult to see how the animals' subsequent drinking would be affected. Changes in the concentration of the extracellular fluid, however, have secondary effects on intracellular fluid, and so cellular function is finally influenced. In the present case this end result would be intracellular dehydration (6).

If the hypertonic glucose solutions do have their effect on later sugar drinking through the mechanism of hypotonic fluid withdrawal in the stomach, then the following sequence of events might be expected in normal sugar-drinking behavior. When the animal drinks a hypertonic glucose solution (more concentrated than 5.3 per cent in the present work), the first small volume that is ingested withdraws hypotonic fluid into the stomach. This osmotic effect of the ingested sugar solution results in intracellular dehydration at some point in the body. When this dehydration has proceeded far enough, it terminates the further drinking of the hypertonic glucose solution. This will be recognized as a type of control generally referred to as a negative feedback system. The stomach-load data show that the more hypertonic the load, the more vigorous is this effect; and, comparably, the more hypertonic the test solution, the more rapid is the termination of the maximal rate of drinking.

It is pure speculation at present to consider where in the body the crucial intracellular dehydration might take place. It would be interesting to know whether it is a direct effect on the peripheral taste receptors or on some more central part of the nervous system. Recording from taste fibers in animals under varying degrees of dehydration and employing variously concentrated solutions for stimuli would be one possible way of getting at the peripheral part of this problem. From the standpoint of the central nervous system, it has already been suggested that there are receptors in the supraoptic area which are sensitive to changes in the osmotic pressure of the circulating blood (21).

Finally, you will recognize that the dehydration process suggested here is a nonspecific mechanism to account for the operation of a specific hunger. This idea necessarily raises a question. Do some of the previously reported instances of specific hungers only appear to be specific because of the limited choice of substances offered the animal? In other words, is it possible that to some extent the substance-specific behavior that has been noted in the past is due to the fact that the animal has been offered specific substances? Pending experimental checks of the generality of this notion, it can only be offered now as a point to be kept in mind in future research in this area.

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APERIODIC FEEDING BEHAVIOR IN THE ALBINO RAT[1]

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Hunger, as evinced in the albino rat, has long been assumed rhythmical or cyclical in nature. To a large extent this assumption is based on Richter's discovery (8) that food-deprived rats exhibit a 2-hr. cycle of activity, as well as his subsequent finding that eating shows a 2- to 4-hr. cycle when food is available. The confirmation of these findings and the establishment of a relationship between feeding, activity, and the contractions of the stomach not only substantiated this assumption but offered strong support to the gastric theory of hunger. Although more recent evidence (6, 12) casts grave doubt on the belief that stomach contractions are the ultimate cause of food intake, there has been little or no challenge of the hypothesis that "hunger" is truly cyclical. If hunger is operationally defined in terms of the instrumental act of approaching food or the consummatory response of food ingestion (4, 7), several reports (1, 2, 3) suggest that feeding behavior is under the control of numerous environmental variables and, when free of these factors, may be essentially aperiodic.

The present study was undertaken to measure the feeding or hunger rhythms of the albino rat in an experimental situation in which the influence of several environmental factors was held at a minimum. Although the title betrays and anticipates the results, under these conditions little or no evidence of cyclical or rhythmical feeding was obtained.

METHOD

Subjects and Apparatus

The *S*s employed were 50 experimentally naive albino rats from the colony maintained by the Stanford Psychology Department. Half the *S*s were male and half were female. The ages ranged from 60 to 90 days at the start of the experiment, and the average animal weighed 134 gm. The animals were housed in 50 individual living cages of uniform materials and dimensions and so constructed and arranged that social cues were eliminated. Each cage was fitted with a detachable food box at one end and a water bottle at the other end. Hinged metal doors opening from the inside of each cage allowed the animals to gain entrance to the food boxes. Lever-arm microswitches were mounted above each door in such a fashion that a monitoring circuit was closed at each opening of the hinged door. This arrangement is a variation of Skinner's (9) apparatus for studying feeding. Since the food box was set slightly below the floor level of the cage, the rats had to withdraw from the food box before eating. Food consisted of the standard Purina Dog Chow processed so that ten pellets of standard size and weight constituted 1 gm. of food.

The experiment was conducted in a large room from which all external illumination was excluded. Constant and uniform internal illumination was assured by six 120-w. bulbs mounted in the experimental room in such a fashion that all 50 living cages were constantly and uniformly illuminated. Illumination was maintained continuously, both day and night, for the entire course of the experiment. Temperature variations were controlled by small electric heaters thermostatically regulated to maintain a room temperature of 80° F.

Twenty-four-hour records of the animal's feeding behavior were made by an Esterline-Angus multiple-unit ink recorder. This apparatus was situated so as to make any possible effects of the sound of its operation negligible. In order to rule out any further disturbances due to extraneous noise, the experimental room was closed except for times when *E* fed and cared for *S*s.

Procedure

On the first day of experimental adjustment the *S*s were placed in the individual cages and provided with water and 30 gm. of Purina Chow in the prepared form. The hinged door of each individual cage was lifted and fixed, allowing the *S*s an unobstructed view of the food pellets. The pellets were of such size that not only did the rat have to reach down into the food box to obtain them, but it was able to procure and eat only one pellet at a time. Hoarding of the pellets was prevented since the wire mesh openings of the cage floor were larger than the pellets. If the rat dropped a pellet, it could not retrieve it. This necessitated the placing of small tin pans beneath the cage floors in order that the number of unconsumed pellets could be determined. After four days of adjustment to the food pellets and feeding from the food boxes, the hinged doors were lowered, thus making it necessary for the animals to push the door outward in order to obtain the pellets.

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[1] This paper is adapted from a thesis presented to the Department of Psychology of Stanford University in partial fulfillment of the Ph.D. degree. I am indebted to Drs. D. H. Lawrence and Calvin P. Stone for their advice and criticism, and to the Nutrition Foundation of New York, New York, for financial support.

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During the ten-day experimental period 24-hr. records of the feeding behavior were taken. Each food box was supplied with 30 gm. (300 pellets) of food every morning, and every water bottle was filled. The food and water were checked once every 12 hr. to insure a constant ad libitum supply.

Prior to each feeding the food was weighed for each *S* individually and again following collection of spillage and remains at the end of the 24-hr. feeding period.

Esterline-Angus records of the feeding behavior were taken on 20 *S*s each day for the ten-day period. Different *S*s were measured each day, each *S* being measured equally often throughout the observation period.

Measuring and Scoring Procedure

The circuits of the Esterline-Angus recorder are monitored so as to permit one to obtain continuous records of both the time and rate of the feeding behavior. It is thus possible to obtain measures of the amount consumed, the time consumption occurred, and the rate of consumption. Although the specific designation of a feeding period is somewhat arbitrary, the following criterion was employed: If at least three openings occurred, separated by no more than 5 min. between openings, a feeding period was scored. If at least 15 min. elapsed between a group of three or more openings, two feeding periods were scored. Measurements were made over a 24-hr. period starting at 8.00 A.M. The scoring procedure was as follows: If a feeding period began in one hour and extended into the next hour, the hour in which the feeding period began was considered the hour in which the period occurred. The time between successive feeding periods, however, was computed in minutes elapsing. On occasions wherein several openings occurred close together, followed by a period of less than 15 min., and then several more openings occurred, the openings were still scored as one feeding period according to the 15-min. criterion. Evidence that this scoring procedure was clearly effective in portraying the nature of the feeding behavior was furnished by the close correspondence of the number of openings and the measure of the amount consumed, obtained by weighing the food remaining in the food box.

RESULTS AND DISCUSSION

The amount of food consumed per 24 hr. for the ten-day ad libitum feeding period, obtained by weighing the food remaining, totaled 11.90 gm. The mean amount consumed, obtained from the Esterline-Angus records, totaled 14.43 gm., revealing a discrepancy of only 2.53 gm. between the measures. This discrepancy was well within the range of spillage. It would seem evident that the *S*s opened the food box only to eat. The average amount consumed, the amount consumed at each feeding period, the number of feeding sessions, and the time between feeding sessions for the ten 24-hr. periods are presented in Table 1.

Although the average time between feeding sessions for all the *S*s was approximately 2 hr. (125.61 min.), the variability is so high (average *SD* = 92.54 min.), that this mean time between feedings does not adequately describe the behavior.

In order to illustrate the arhythmicity characterizing all *S*s, the individual means for a random sample of 12 *S*s measured for four days are presented in Table 2. While the aperiodic nature of the feeding behavior is indicated by the large *SD*'s, other methods are available for discovering randomness or a lack of randomness in sequences of observations (5). These methods assume that the observations constitute a random sequence and then determine a function of the observations for testing the randomness of the sequence. If a set of values of a variable has been obtained by taking samples at regular time intervals, and if a trend or nonrandom pattern exists in the sequence of values, the fact can be discovered by studying the runs of *X*'s and *Y*'s that result from the sequence. In the present instance if nonfeeding periods are assigned the letter N and the feeding periods the letter F, in a regular cyclical pattern the runs would tend to be of uniform length. Since the study of runs proves to be particularly useful in testing for randomness of data that have been ordered with respect to time, the data from the sample of 12 *S*s measured for four days was subjected to this type of analysis. Of the 12 *S*s only 4 proved to be nonrandom. Although such an analysis indicates randomness or nonrandomness, it does not indicate the nature of the periodicity. Accordingly, the data of the 4 nonrandom *S*s were analyzed further.

The four 24-hr. periods of each of the *S*s were tested for the occurrence of feeding or nonfeeding in a given hour against all the possible 4-hr. combinations of feeding or nonfeeding. This breakdown analysis is presented in Table 3. As can be seen from the distribution, no evidence of cyclical feeding appeared. It might be objected that Subject

1, for example, ate on a 3-hr. cycle for one 12-hr. period but showed random feeding for the rest of the period. To illustrate the lack of such short-term periodicity, the entire run was as follows:

NNFN FNFN NNNF FNFF NNFN FNFN
NNNF FNFF NFNF FNNN FNNF NFNN
FNNN FNNF NNFF FNFN NNFN NNNF
NFNN FNFN FFNF NFNF FNNN FNNN

While the aperiodic nature of the feeding seems evident, the possibility that a relationship existed between the amount of food ingested and the time of self-imposed deprivation was also examined. The aperiodic nature of the feeding might well be because only a few pellets were consumed on each occasion, necessitating frequent returns to the food box, whereas if a large amount were consumed

TABLE 1

Feeding Behavior for Ten-Day Observation Period

($N = 50$. Twenty *S*s, 10 males and 10 females, were sampled each day. Each *S* was measured equally often over the ten-day period.)

DAY	MEAN GRAMS CONSUMED PER FEEDING PERIOD	RANGE	MEAN NO. OF FEEDING PERIODS	RANGE	MEAN NO. MINUTES BETWEEN FEEDING PERIODS	RANGE	*SD*
1	1.30	.82–1.86	11.4	7–16	127.4	65.7–187.3	97.2
2	1.28	.78–1.67	10.8	9–14	118.5	86.5–138.7	60.5
3	1.35	.92–2.15	9.8	8–15	113.3	72.6–172.3	67.4
4	1.22	.67–1.88	12.4	7–14	110.7	61.2–173.1	106.5
5	1.30	.78–1.72	11.8	7–16	134.7	67.6–188.0	108.6
6	1.23	.65–1.94	12.2	6–18	138.7	92.4–272.5	110.6
7	1.32	.80–1.71	11.3	8–14	115.4	71.4–173.2	89.5
8	1.19	.81–1.58	11.6	7–15	120.8	77.5–156.5	88.3
9	1.38	.79–2.21	9.2	4–14	132.8	76.8–167.7	103.4
10	1.37	.89–2.14	10.9	6–15	143.8	72.5–191.0	93.4
Total	12.94		111.4		1256.1		925.4
Mean	1.29		11.1		125.6		92.5

TABLE 2

Test for Periodicity of Feeding and the Individual Means for a Random Sample of 12 Subjects, 6 Males and 6 Females, Measured for Four Days

SUBJECT	NO. SESSIONS PER DAY	MEAN GRAMS CONSUMED PER FEEDING PERIOD	*SD*	MEAN NO. MINUTES BETWEEN FEEDING PERIODS	*SD*	RANDOMNESS TEST†			
						FEEDING PERIODS	NON-FEEDING PERIODS	RUNS	*p*
1	9.8	1.33	.35	125.2	60.4	39	57	61	.001*
2	7.8	1.27	.29	150.8	122.4	39	58	53	.127
3	9.0	1.72	.59	134.8	89.9	31	65	46	.250
4	14.3	.85	.33	90.5	49.6	48	54	52	.484
5	12.3	.78	.25	104.8	74.4	39	59	35	.006*
6	12.8	1.14	.62	81.1	69.4	36	61	57	.008*
7	12.0	.98	.38	92.9	67.5	38	58	45	.341
8	8.8	1.36	.38	131.6	49.3	57	42	55	.119
9	7.5	1.69	.59	171.5	92.9	49	51	53	.337
10	9.0	1.41	.37	126.9	103.6	38	60	51	.227
11	9.8	1.18	.71	137.3	109.9	32	59	36	.011*
12	11.8	.94	.35	108.2	65.4	42	55	47	.371

* Statistically significant value.

† Since the values of F and NF are larger than 20, a normal approximation may be used. The mean in this instance is $\frac{2N_1N_2}{N_1+N_2}+1$ and the variance is $\frac{2N_1N_2(2N_1N_2-N_1-N_2)}{(N_1+N_2)^2(N_1+N_2-1)}$. The expected mean (number runs) minus the obtained mean (number runs) divided by the variance is the equivalent of the critical ratio. When the table of the normal curve is entered, this value gives the probability of occurrence.

at one feeding, longer time intervals would elapse between feedings. Accordingly, for the sample of 12 *S*s the product-moment correlation coefficients between the amount of food ingested and the time of self-imposed deprivation for the four-day period were determined. No significant relationship between the amount consumed and the self-imposed deprivation time was obtained for any of the 12 *S*s.

TABLE 3

Test for Periodicity of Feeding in the Four Nonrandom Subjects

PRESENCE OR ABSENCE OF FEEDING*	SUBJECT AND SIGNIFICANCE LEVEL			
	1 $p = .001$	6 $p = .008$	5 $p = .006$	11 $p = .011$
1. NNNN		1	6	4
2. NNNF	3	1	1	5
3. NNFN	3	1		1
4. NFNN	2	8	1	1
5. FNNN	4	2	2	3
6. NNFF	1		2	
7. NFFN		1	2	1
8. FFNN		3	2	
9. NFNF	2			
10. FNFN	4	4	1	1
11. FNNF	2	1	1	2
12. NFFF			1	3
13. FFFN		1	1	
14. FNFF	2		1	2
15. FFNF	1	1	2	
16. FFFF			1	1
Totals	24	24	24	24

* N indicates no feeding occurred within a given hour; F indicates feeding did occur within a given hour.

From the results of this experiment it would seem that no well-defined feeding rhythms were in evidence. Arhythmicity characterized all individual *S*s. It must be assumed, therefore, that no rhythms existed in any of the *S*s prior to the introduction of the environmental controls, i.e., constant illumination, individual isolation, controlled temperature, ad libitum food and water, etc., or that the installation of the controls eradicated any feeding rhythms that were present.

Since Richter (8) and Slonaker (11) have reported the existence of 2- to 4-hr. feeding cycles and these observations have been confirmed by others, the latter alternative is favored. The present finding is similar to that of Brody (1), who has reported the extinction of the rat's diurnal metabolic rhythm following a week of continuous light and continuous feeding. The present results are also in line with Wolf's (13) finding that mice reared in darkness from birth failed to develop a diurnal activity rhythm. If feeding rhythms strongly depend upon certain cues from the environment, a removal or alteration of these cues would result in the disappearance of the cyclical behavior. At least, in this experiment it is believed some such dependency existed.

The fact, however, that the average time between feedings was approximately 2 hr. and the variability was so extreme strongly suggests that prior assumptions of cyclical feeding behavior in natural surroundings are largely the result of averaging rather than conclusive demonstration of rhythmicity in feeding. Until further experimentation clarifies the extent to which feeding rhythms depend or do not depend upon particular environmental changes, it is suggested that the alternative hypothesis of aperiodicity in feeding be seriously entertained.

SUMMARY AND CONCLUSIONS

Records of the feeding behavior of 50 albino rats were obtained for a ten-day period under uniform environmental conditions. The subsequent analysis of the feeding behavior revealed that no feeding rhythms were in evidence for any of the 50 *S*s. It is suggested that feeding rhythms strongly depend upon cues from the natural environmental cycles such as temperature and illumination. In addition, social cues and prior feeding experience may be contributing factors. When these cues are removed or minimized, aperiodicity characterizes the feeding behavior.

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SOCIAL FACILITATION OF EATING BEHAVIOR IN PUPPIES AFTER SATIATION

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Recent experiments by Ross and Ross on solitary versus group feeding (2) and group feeding after satiation (3) indicate that social facilitation is a significant factor in eating behavior among dogs. In both experiments it was evident, however, that there were wide differences in the effect of social facilitation upon the animals. Some dogs ate the greater amount of their total intake alone, while others ate less of their total intake alone and were greatly influenced by the group. It is possible that there were constitutional variations among the dogs which would explain the differences in susceptibility to social facilitation. Ross indicated that dominance might be one of the important factors, but found no direct relationship between dominance and food intake under the conditions of his experiment. If animals were used in which there were wide differences in dominance appearing early in life, the importance of this factor might be emphasized. Among the hybrid animals used at the University of Georgia, dominance-submissiveness variation has been one of the most significant differences found, and these animals seemed to be good material for further analysis of this problem.

PROBLEM

The present experiment investigated the effect of group feeding in puppies following satiation in individual feeding, with emphasis on the relationship between dominance and variability in food intake under each condition.

METHOD

Subjects

The *S*s of the experiments were five F_2 generation beagle-terrier hybrids, born on March 23, 1952. The puppies were 35 days old at the beginning of the experiments and 75 days old at the completion of the study. They were born in the laboratory and were used in studies on sensitivity and movement patterns during the first four weeks of life. The food used in the experiments consisted of Purina Kibbled Meal soaked in warm water. Every attempt was made to prepare the food with the same consistency from day to day.

Procedure

In the first part of the experiment each animal was fed once a day in the late afternoon for 20 days. The animal was weighed on an autopsy scale graduated in 10-gm. units, and then placed in the experimental room and permitted to eat all the food it desired. The animal was weighed again to determine the amount of food eaten. The second weighing occurred only after the animal walked away from the pan and refused to return to it.

After the five animals had been fed all they would eat alone, they were brought back into the room as a group. Each animal was weighed again to determine the weight loss, if any, due to defecation and urination during the interval. A large pan of food was placed before them, and again they were permitted to eat all they wanted. As a rule, alone each dog would eat all it wanted in from 5 to 8 min. Since the dog which was fed first had a greater interval of time between the first and second feeding, the dog which was fed first on one day was fed last on the following day. In this manner all dogs were fed in the first, second, third, fourth, and fifth positions four times.

Control Tests

Since it was possible that an animal would eat more food in the second presentation in any case, control tests were run for ten days in which each dog was returned to the room singly a second time and permitted to eat again. The same general order of feeding was followed during the control tests as in the experimental series.

Following the above tests an analysis was made of dominance order among the puppies by the procedure which has been described previously (1). It involved bringing the animals together first as a group and later in combinations of two and three, to determine which animal would obtain food in a competitive situation. The interest was in determining if the dominance order was important in eating behavior in the above tests.

RESULTS

The data have been handled by calculating the chi-square values between the number of times each dog ate more food alone or in social feeding in the experimental tests, and the number of times each animal ate more food in the first or second feeding in the control tests. For example, animal 41 ate more food alone 3 times in the experimental tests, while in 17 cases the animal ate more with the group. In the control tests this dog ate more food in the first feeding in 9 of the 10 tests. The same data were obtained on all animals. The chi-square values between the experimental and control data are shown in Table 1.

The values for dogs 41, 44, and 45 are significant beyond the 5 per cent level. For animals 42 and 43 the values are not significant. Animals 42 and 43 seemed to be less dependent on group action and less affected by the group in eating behavior than the other three dogs.

TABLE 1
Chi-Square Values between the Experimental and Control Tests

DOG.....	41	42	43	44	45
χ^2	15.64	1.47	2.14	5.47	4.55

Dominance and Eating Behavior after Satiation

When the dominance order of the animals was determined, one difference was observed which may be important for the variation in susceptibility to social facilitation. Animals 42 and 43 were the dominant members of the group, with 42 slightly more dominant than 43. The order of dominance below these two animals was as follows: 45, 44, and 41. The results suggest that the dominant dogs were less affected by social stimulation and that the least dominant dog was most affected by the group.

DISCUSSION

The relationship between dominance and eating behavior was surprising, since it was expected that the dominant animals would eat a higher percentage of food in the social situation. Competition was not involved in the eating behavior since the pan was large enough for all dogs to eat together, and none could be pushed away from the food. It does not seem reasonable to assume that there was a stronger hunger drive in the dominant animals and that for this reason they ate a greater part of their total food intake during the first presentation of food. This may have been a factor, however. Constitutional differences may be important. It is possible that the dominant animals are in general more vigorous, independent, and enter into all behavior with a greater energy factor than the submissive animals. This variation between dominant and submissive animals has been entirely overlooked. In any case, the variation in vigor with which the dominant animals enter into each activity in comparison with the submissive dogs is a problem which warrants further study.

SUMMARY

For 20 days five second-generation beagle-terrier hybrid puppies, 35 days old, were fed all the food they would eat individually and then, immediately, they were presented with food again as a group. For 10 days control tests were conducted in which each animal was fed twice individually. The chi-square values were determined between the number of times each animal ate the most food in social or individual feeding in the experimental tests, and in the first or second feeding in the control tests. These values were significant within the 5 per cent level of confidence in three animals, suggesting influence of group action on eating behavior, and not significant in two animals. The latter were the dominant members of the group. The results indicate that dominant animals are less dependent upon, and less affected by, social facilitation. It is suggested that the dominant animals have constitutional factors which cause them to enter into all behavior in a more vigorous and active manner. Further experiments need to be done, however, before this is conclusive.

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ELEVATION OF ACTIVITY LEVEL IN THE RAT FOLLOWING TRANSITION FROM AD LIBITUM TO RESTRICTED FEEDING

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The pioneer work of Finger (2) and of Finger and Reid (3) has demonstrated a "satiation syndrome" in the white rat. An animal deprived of food or water, for a day or more, not only exhibits a progressive elevation in activity level, but, when food or water is restored, displays a radical depression in activity to a point well below normal. The latter effect is the satiation syndrome, and it is testimony to the fact that activity level (and, presumably, motivational level) is not a simple function of the animal's nutritional regimen.

As Finger indicates, this finding has important methodological implications. One of them might be as follows: Rather generally, learning experiments employ as *S*s white rats under something like a "23-hr. hunger drive"; the animals are deprived of food for 23 hr. and run and fed during the twenty-fourth hour of each successive experimental day. It is assumed that the daily periods of deprivation, being equal in length, induce equal motivation during the daily running periods, that no cumulative effects arise, and, thus, that the entire learning process is uncontaminated by systematic changes in level of drive. This assumption may be unjustified. The experimental animals are customarily shifted from an ad libitum regimen to the feeding schedule characteristic of the problem only a few days before experimentation begins; and, if it should be true that such a shift is followed by a gradual alteration of drive level, any experimental data generated might well be distorted by the change.

The purpose of the study reported here was to explore this possibility. Specifically, the problem was to measure changes in general activity in the rat following transition from unlimited feeding to a 23-hr. per day deprivation cycle. Toward this end, two separate experiments were performed, and they will be described individually below.

EXPERIMENT I

Method

The *S*s for this experiment were, originally, ten male albino rats from the colony of the psychological laboratories of The Pennsylvania State College. The age of each animal at the beginning of the study was 65 ± 3 days. Seven animals completed the experiment and are reported upon here.

The apparatus consisted of ten standard Wahmann activity drums, each separately mounted and each providing a small, stationary living cage (cf. 5, p. 53). The cages were provided with water bottles, and food was furnished in large, earthenware dishes. A counter on every wheel registered revolutions in either direction. The wheels were equated for frictional torque by Lacey's method (4).

The drums were located in a light-tight room, upon a macadamized floor which prevented transmission of vibration between drums. Auditory interaction between animals was controlled by surgery, as described below. Room temperature was satisfactorily stable.

The experiment proper was preceded by an adaptation period of 40 days. During this time the animals were in the drums, with food (wet mash of Rockland Rat Diet) and water constantly available. Activity records showed the usual initial increase from day to day, with an ultimate stabilization.

On the twenty-second day of the adaptation period, the animals were removed from the cages briefly, anesthetized lightly, and deafened by surgical operation: a probe was passed through each tympanic membrane and rotated to disrupt the ossicular chain. Behavioral observation and gross autopsy suggested that this operation was successful; on the other hand, one animal was lost almost immediately, evidently from infection introduced at surgery. Two additional animals died later from undetermined causes.

Immediately following the adaptation period, and starting at 12:00 M., the base period began. For seven successive days the room was isolated and completely dark, save for four daily entries: briefly and by weak flashlight at 6:00 P.M., 12:00 P.M., and 6:00 A.M., to obtain counterreadings; and for an hour and a half under full illumination from 10:30 A.M. to 12:00 M., to care for the animals and to replenish food and water, as well as to determine counterreadings. Food and water were continuously available during the base period.

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[1] This article is based upon research for the master's thesis performed by the junior authors under the direction of the senior authors. The writers are indebted to Dr. E. B. Hale, who instructed them in the surgery described herein.

Temperature records showed a range of 71.5 ± 3.5° F. for the entire seven days.

As soon as the base period had terminated, and thus again at 12:00 M., the experimental period began. Animals 1, 8, and 10 were placed upon a restricted-feeding schedule; they were allowed access to food only during the period 10:30 A.M. to 11:30 A.M. each day (the time 11:30 A.M. to 12:00 M. was spent in cleaning cages, etc.). For the remaining animals, and in all other respects, the procedure continued as during the base period. This phase came to an end at 12:00 M. after just seven days, and a recovery period, also of seven days, followed; during it the base-period routine was followed for all animals. Immediately after this recovery period, animals 2, 4, 7, and 9, previously control animals, were placed on the regimen of restricted feeding. Again, this phase embraced exactly seven days; again, there was a recovery period, this time of three days. The experiment was then terminated, the animals were sacrificed, and autopsies were performed. During the entire experimental period, the range of temperatures in the animals' room was 71.5 ± 2.5° F.

It is evident that the research design was one of counterbalanced order, intended to relieve the data of artifacts owing to changes in age, temperature, etc. The base period was instituted in order to determine for each animal a "normal" rate of running in terms of which subsequent performance could be expressed; it was hoped thus to narrow the range of individual differences.

Results and Discussion

It will be noted that each experimental "day" began and ended at 12:00 M. Activity readings were always taken at 12:00 M., 6:00 P.M., 12:00 P.M., 6:00 A.M., and 10:30 A.M. The period 10:30 A.M. to 12:00 M. was ignored in all activity records and computations, inasmuch as this was the period during which *E* was about the animals. There thus remain, for each day, four successive periods for which records were kept separately: 12:00 M. to 6:00 P.M., 6:00 P.M. to 12:00 P.M., 12:00 P.M. to 6:00 A.M., and 6:00 A.M. to 10:30 A.M. Food was constantly available, except when an animal was on the restricted-feeding schedule. In the latter case, food was available only during the interval 10:30 A.M. to 11:30 A.M. each day; by 10:30 A.M. the animal had experienced 23 hr. of deprivation.

In analyzing the activity records, the first step was to compute a base rate for each animal: the total number of recorded revolutions during the base period was divided by the total number of hours during which records were kept. The animal's base rate was thus expressed in terms of revolutions per hour.

Each animal's activity during the experimental period was then measured in the following manner. The animal's mean rate, in revolutions per hour, was computed for each period of each day. This mean rate was then divided by the animal's base rate to obtain a figure in terms of percentage of base rate. Finally, all such figures were plotted against their corresponding daily periods for: (*a*) the seven days during which the animal was on a restricted regimen, plus the subsequent three days (experimental condition); and (*b*) the seven days during which the animal acted as an ad libitum control on other, restricted animals, plus the subsequent three days (control condition).

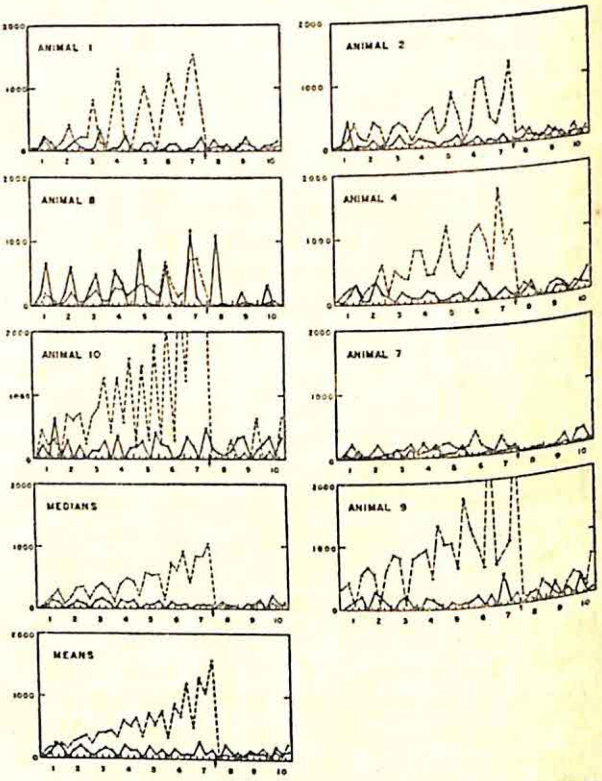

FIG. 1. Running activity, in percentage of base rate, during each period of each day. Broken curves, experimental condition; solid curves, control condition. (Experiment I)

The results of this procedure are shown in Figure 1. The individual records for animals 1, 8, and 10, which acted first as experimental and then as control cases, appear in the left-hand column of graphs. The records for animals 2, 4, 7, and 9, whose schedule was the reverse, are presented in the right-hand column. Abscissas represent days and daily periods; ordinates represent activity level in percentage of base rate. Broken curves indicate the experimental condition, and solid curves the control condition. The end of the seventh day, where restricted feeding gave way to an ad libitum recovery regimen in the experimental condition, is indicated by a small arrowhead on each abscissa.

In general, the individual records show stable control curves at about the expected level of 100 per cent. The possible exceptions to this generalization occur mainly among those animals (1, 8, and 10) which served initially in the experimental condition and thus, one may hazard, suffered a mild but rather lasting disruption of activity. The typical curve for the experimental condition shows a steady increase in activity. Sometimes, as for animals 7 and 8, this rise is not noteworthy. Occasionally, as for animals 9 and 10, it is rather spectacular; animal 10 attained a rate of almost 5,000 per cent during one period. Generally speaking, the return from restricted to ad libitum feeding at the end of the seventh experimental day brought a precipitous decline in activity, but the satiation syndrome is not immediately suggested under the present experimental conditions.

Because it is difficult to show central tendency when the number of cases is small, the individual data were summarized in two ways. The median activity rate for each daily period was determined, and the mean rate was also determined. The results are shown appropriately in the two lower graphs in the left-hand column of Figure 1. As it happens, the two statistical treatments come to much the same result in the end, although the means tend to be inflated during the final days of the restricted-feeding period by the extreme records of animals 9 and 10.

Both the medians and the means are quite stable for the control condition, there being the usual repetitive daily cycle of activity. The records for the experimental condition, on the other hand, show an exaggeration of the normal daily cycle imposed upon a sharply rising base line. (Each animal's mean hourly rate, in terms of percentage of base rate, was determined for the entire seventh experimental day and for the entire seventh control day; in spite of the small number of *S*s and the wide variation from animal to animal, the mean difference in activity was significant, by *t* test, at the .05 level.) At the seventh day, furthermore, experimental activity was still increasing steadily; additional investigation to discover its ultimate level was clearly indicated.

There is, especially in the graph of the means (Fig. 1), a hint of the satiation syndrome. The mean difference in activity for the eighth day was, however, far from statistically significant. Apparently an experimental condition of daily (even though restricted) feeding has somewhat different effects from an experimental condition of total deprivation (2).

EXPERIMENT II

Experiment II was run to discover the ultimate level of the activity curve, as well as to verify the previous findings. The major changes made in the experimental conditions were: (*a*) to utilize separate experimental and control groups rather than employing the counterbalanced design used in Experiment I, and (*b*) to substitute a single daily reading of the activity records for the four made previously. The number of activity wheels available (ten) necessitated running the study in two consecutive sessions in order to provide a suitable number of *S*s.

Method

The *S*s were originally 20 male albino rats obtained from the colony of the psychological laboratories of The Pennsylvania State College. The 5 experimental and 5 control animals used in session 1 were 93 to 94 days old at the beginning of the base period; the animals used in session 2 were 73 to 75 days old at the beginning of the same period. Two control animals during session 1 and 1 during session 2 were eliminated from the study when their records indicated an activity of only one to five revolutions per day. Two experimental animals died during session 2. As a result of these eliminations, the final *N* was 15.

The activity wheels used in Experiment I were also used in Experiment II; the wheels were recalibrated to record amounts of frictional torque equivalent to that used in Experiment I.

All animals were first deafened and given one week to recover from the effects of the operation. The surgical technique used in deafening the animals has been previously described. The animals were then placed in the wheels for an adaptation period of 14 days. Food and water were constantly available during this period.

During the adaptation period the animals were assigned to either the experimental or control group. This was done as follows: Two animals were selected at random and a coin tossed to determine whether the first animal of the two was to be placed in the experimental or control group. This procedure was repeated until all ten animals were assigned. During session 2, it was arranged that the experimental animals were placed in wheels which had been used by the control animals of session 1, and vice versa.

Immediately following the adaptation period, the base period began. The procedure and experimental conditions were identical to those described in Experiment I, except that the entries into the experimental room at 6:00 P.M., 12:00 P.M., and 6:00 A.M. were eliminated.

The experimental period immediately followed the base period and continued for 21 days. The control animals remained on the base-period regimen. The experimental animals were placed on a restricted-feeding schedule and permitted access to food only from 10:30 A.M. to 11:30 A.M. each day. Water was continuously available. The range of temperatures throughout session 1 was 76 ± 7°, with daily fluctuations in temperature rarely exceedingly 3°. The temperature throughout session 2 was 70 ± 4°, with daily fluctuations never exceeding 2°.

Results and Discussion

The steps taken in the analysis of each animal's activity were similar to those described in Experiment I. Each animal's base rate (now in revolutions per day) was obtained by totaling the number of recorded revolutions during the seven-day base period, and dividing by seven. The animal's activity for each experimental day was then divided by the base rate in order to obtain a daily figure expressed in terms of a percentage of the base rate.

The means for the experimental and control animals for each day of the experimental period are indicated in Figure 2. Analysis of the results for the first seven-day period reveals findings which are almost identical to those obtained during Experiment I, thus providing confirmation of these findings. As the plots indicate, activity for the experimental animals continues to rise even after the first week, reaching the asymptote at approximately the twelfth day. At this point, these animals averaged 1,438 per cent of their base rate. Records of the control animals do not reveal the same systematic increases, although their activity over the experimental period was consistently greater than that of their base rate. Their peak activity was made on day 14, when they recorded 223 per cent of their base rate. Careful examination of the records, however, indicates no covariance between the fluctuations of the experimental and control groups.

Although Figure 2 reveals gross differences in behavior between the control and experimental animals, it was felt that statistical analysis would, nonetheless, be appropriate. The large difference between the variances of the experimental and control groups necessitated the use of the Festinger technique (1) to test for differences in activity. Each animal's daily running activity, in percentage of base rate, was totaled and a mean obtained for the 21-day period. Appropriate rankings based on these means were then given to the experimental and control animals. Results indicated that the difference between the experimental and control groups was significant beyond the .01 level of confidence.

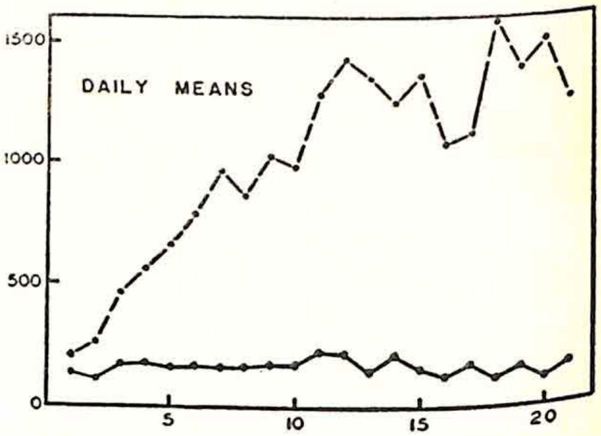

FIG. 2. Mean daily running activity, in percentage of base rate. Broken curve, experimental condition; solid curve, control condition. (Experiment II)

SUMMARY AND CONCLUSIONS

Two experiments, employing a total of 22 albino rats, were conducted to determine the effect of an extended restricted-feeding schedule on activity level. The control condition was one of free access to food and water; the experimental condition was one of free access to water but 23-hr. per day food deprivation. Visual, auditory, and vibrational factors were suitably controlled, as was temperature.

Although activity during the control condition remained relatively stable, mean daily activity during the experimental period rose to more than 1,400 per cent of normal, reaching this level at the twelfth day of restricted feeding. The rise seemed to take the form of an exaggeration of the normal daily-activity cycle, imposed upon a rising base line. Finger's "satiation syndrome" was not clearly present, but it was not necessarily to be expected.

Methodological caution is indicated in those studies which essentially duplicate the motivational conditions of the present experiment, yet assume no systematic change in strength of drive.

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THE EFFECTS OF COMBINING HUNGER AND THIRST MOTIVES IN A DISCRIMINATION HABIT[1]

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The effects of combining motives upon learning efficiency is an old problem. It is also a problem of considerable practical significance as, for example, in the areas of industrial production and child training. And yet there is no clear-cut experimental evidence as to whether or not the combination of two motives results in a learning efficiency which is greater than that of the more effective of the two motives. Muenzinger and Fletcher (1) combined hunger-food with shock-escape in the acquisition by white rats of a visual discrimination habit and found that the resulting efficiency was no greater than that of shock-escape alone. The *E*s suggest that: "*It is quite possible that this is a fundamental principle of activity, namely, that the combination of motivating factors results not in a summation of their effects but in an effect equal to that of the stronger factor*" (1, pp. 88–89). However, they are also careful to point out that their results do not unequivocally support this conclusion. It is possible, they say, that the shock-escape motive is one which produces maximum learning efficiency so that any combination of shock-escape with any other motive would not produce an increased efficiency. In order to obtain unequivocal results, it would therefore be necessary to employ motives which singly do not produce maximum efficiency. This is the method used in the present study. For only if one uses relatively weak motives, might one expect to find that their combination would produce a greater learning efficiency than that of either motive alone.

Certain theoretical considerations led the writer to predict, however, that this would not happen. In an unpublished paper, "A Theory of Motivation," Muenzinger proposed that the principle of figure and ground describes the fundamental organization not only in perception but in other aspects of behavior. "It would be a reasonable hypothesis," Muenzinger writes, "to assume the operation of the principle of figure and ground not only in discrimination, but also in motivation, performance and affectivity." After discussing the latter two, he continues, "in human motivation complexity of motives is the rule and yet here, too, we must assume the operation of figure and ground, namely, that one motive stands out as the dominant one at any time while the others form the relatively neutral ground. Given the close functional interrelation between motivation and discrimination, what else could we assume?"

On such a theoretical basis the hypothesis underlying the present study can be formulated as follows: Whenever we combine two or more motives, one of them will stand out as the figure and manifest itself in discrimination and the efficiency of performance. There is no additive effect. If we had two motives of equal strength, as measured by efficiency of performance (speed, trials, errors), the combination of the two should produce a level of efficiency as great as that produced by a single motive. And if we combine two motives of unequal strength, we should expect a level of efficiency no greater than that of the stronger motive, or perhaps one lying between that of the weaker and that of the stronger motive.

In general terms, our problem will be to study the effects of combining relatively weak motives upon learning efficiency. Specifically, we shall employ two strengths each of hunger-food and thirst-water motives and their four combinations in the acquisition of a black-white discrimination habit by hooded rats.

METHOD

The apparatus consisted of a Y-shaped discrimination box with black (positive) and white (negative) cards at the ends of the choice alleys during the learning series, and gray cards during the preliminary training.[2]

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[1] This is a portion of a thesis submitted in partial fulfillment of the requirements for the Ph.D. degree at the University of Colorado. The author wishes especially to thank Dr. Karl F. Muenzinger for his generous advice and encouragement.

The *S*s were 80 naive, male and female, hooded rats from the colony at the University of Colorado laboratory. There were 47 males and 33 females. At the beginning of the experiment they were approximately 60 days old. There were 10 *S*s in each group.

Two groups were trained with 6-hr. and 23-hr. food deprivations, respectively, and two groups with similar water deprivations. The fifth group was subjected to a simultaneous 6-hr. food and water deprivation and the sixth to a 23-hr. food and water deprivation. The seventh group was subjected to a 6-hr. food and a 23-hr. water deprivation, and the eighth to a 23-hr. food and a 6-hr. water deprivation. We thus had four groups with single and four groups with combined motives.

The preliminary training lasted four days during which the *S*s were acquainted with the apparatus with gray cards in the choice alleys.

In the learning series the correction method was used. When an animal made an error, it could not enter the white-paneled door, but had to retrace until it finally entered the goal chamber through the black-paneled door. An error was counted whenever the animal placed both rear legs beyond the elevated barrier at the entry to a choice alley.

On the first four days all animals were given 5 trials per day, so that by the end of the fourth day they had received a total of 20 trials. The sequence of alternations of the black panel was as follows: Day 1, LRRLL; Day 2, RLRRL; Day 3, RLLRR; Day 4, LRLLR. From this time until the end of the experiment the animals were given 10 trials per day with the following sequences on alternating days: LRRLLRLRRL and RLLRRLRLLR.

Latencies, measured by synchronous clocks and microswitches at both doors of the apparatus, were recorded for all experimental trials beginning with the first. The criterion of learning was two successive errorless days of ten trials each.

The food consisted of Purina Dog Chow, a pellet of which was placed in the goal chamber in the condition of food deprivation. In the case of water deprivation the goal was ¼ cc. of water in a 6-mm. glass tube with a 2-mm. orifice. The tube extended 2 cm. into the goal chamber through a hole in the rear wall 1½ in. above the floor of the goal box and in the center of the chamber.

One week before the beginning of the experiment the animals were gradually adjusted to a short eating period. This was true for all groups including the ones on a 6-hr. deprivation, which had food, or water, or both present in the home cages for 18 hr. of the day. On the first day the animals were placed in separate cages in the feeding room and allowed to eat and drink for a period of 3 hr. By the end of the week this period had been reduced to 45 min., and this feeding schedule was maintained until the end of the experiment.

For the animals on a 6-hr. deprivation schedule the incentive (food, water, or both) was removed from their home cages in the morning, and they were run in the afternoon 6 hr. later. Those animals on 23-hr. deprivation never had the corresponding incentive(s) present in the home cages after the experiment began.

RESULTS

Table 1 presents the mean learning efficiencies of all groups in terms of reinforcements, errors, and latencies to reach the criterion. Tables 2 and 3 present the significance of the mean differences for reinforcements and errors.

TABLE 1

Reinforcements, Errors, and Mean Latencies for all Groups to Reach the Criterion

GROUPS*	REINFORCEMENTS		ERRORS		MEAN LATENCIES IN SECONDS
	M	σ^2	*M*	σ^2	
1a H6	105	65	36.0	60.8	9.63
1b T6	134	144	41.7	73.0	17.18
1c H6-T6	121	109	39.5	75.76	11.60
2a H23	78	136	29.9	58.09	7.07
2b T23	73	81	29.6	13.84	3.71
2c H23-T23	79	49	27.6	7.75	4.95
3a H6-T23	86	104	29.6	33.84	4.14
3b H23-T6	83	141	29.2	11.16	3.95

* $N = 10$ per group.

The design of the experiment as a whole permits a statement of the results in terms of four separate comparisons, each of which is concerned with three groups, two with single motives, which were combined in the third group.

Comparison 1, weak hunger, weak thirst, and their combination: Groups 1a, 1b, and 1c. The combination group falls between the single groups in terms of all criteria.

Comparison 2, strong hunger, strong thirst, and their combination: Groups 2a, 2b, and 2c. The combination group is insignificantly poorer than both single groups in terms of reinforcements and insignificantly better in terms of errors.

Comparison 3, strong hunger, weak thirst, and their combination: Groups 2a, 1b, and 3b. In terms of reinforcements the combination group falls between the single groups, and in errors it is insignificantly better than the better of the two.

Comparison 4, weak hunger, strong thirst, and their combination: Groups 1a, 2b, and 3a. In terms of reinforcements the combination group falls again between the single groups, and in errors it is the same as the better of the two.

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[2] Details of construction may be obtained from the author. So also may any other information which is omitted in this article for reason of space economy.

To summarize: In terms of reinforcements the four combination groups are in no case better than the better of the two relevant singly motivated groups. In terms of errors one combination group, 1c, is poorer than the better of the single groups; one, 3a, is the same as the better one; and two, 2c and 3b, are insignificantly better than the better ones of the relevant single groups.

TABLE 2

Significance of the Difference between Trials for a Combination of the Eight Groups Taken Two at a Time

GROUP	1a	1b	1c	2a	2b	2c	3a	3b
1a	—	.001	.01	.01	.001	.001	.01	.01
1b		—	.05	.001	.001	.001	.001	.001
1c			—	.001	.01	.01	.01	.01
2a				—	*	*	*	*
2b					—	*	.02	.10
2c						—	*	*
3a							—	*
3b								—

* Difference is not significant.

TABLE 3

Significance of the Difference between Errors for a Combination of the Eight Groups Taken Two at a Time

GROUP	1a	1b	1c	2a	2b	2c	3a	3b
1a	—	.20	*	.10	.02	.01	.05	.02
1b		—	*	.01	.01	.01	.01	.01
1c			—	.05	.01	.01	.02	.01
2a				—	*	*	*	*
2b					—	.20	*	*
2c						—	*	*
3a							—	*
3b								—

* Difference is not significant.

The latencies show the same relations as the reinforcements (trials to criterion), except in group 3b.

Another aspect of the results deserves special mention. All groups having 23 hr. of deprivation, either singly or in combination, are significantly superior to all groups having only 6 hr. of deprivation, singly or combined in terms of reinforcements and errors. With tension assumed to be an increasing function of duration of deprivation, a comparison of the low-tension with the high-tension groups shows an increased efficiency in performance with an increase in tension.

DISCUSSION

Our principal interest in this experiment was to determine whether a combination of two motives would yield more efficient performance than would either motive used singly. On the basis of a theoretical analysis formulated by Muenzinger it was hypothesized that motives in combination do not produce a resultant tension which is additive in effect; the combination is not like the product of a parallelogram of forces. Instead, the hypothesis proposed here was that motives in combination produce a tension perhaps as great as, but not greater than, the tension of the stronger motive.

The results of the four subexperiments would seem to confirm our hypothesis. Especially striking is the effect of combining the two weak motives of 6-hr. deprivation of food and water. The group with combined motives, 1c, was in terms of all three criteria better than one of the singly motivated groups, group 1b, and poorer than the other one, group 1a. If a combination of motives were to result in a learning efficiency greater than that produced by the better one of the single motives, this should have been the occasion, since there was a large margin between the learning efficiency resulting from the rather weak single motives and possible maximum efficiency in the particular situation used.

A comparison between our low-motivation groups and our high-motivation groups revealed that the groups with high motivation were more efficient in terms of trials, errors, and latencies. Assuming that performance is a function of the tension induced by motivational conditions, our results indicate that the two levels of deprivation used by us produced different degrees of tension in the animals. These results are in accord with those of O'Kelly and Heyer (2).

Space does not permit us to discuss in detail the all important facts of the physiological interrelations of hunger and thirst. Hunger affects water intake and thirst affects food intake. That these facts do not invalidate our results, however, is indicated by the observation that a 23-hr. food deprivation produced the same efficiency, as predicted, whether it was accompanied by a 23-hr., 6-hr., or 0-hr. water deprivation. Some motivation of varying degrees of thirst must certainly have been added by the progression from a 0-hr. to a 23-hr. water deprivation, unless one assumes that the combination of a 23-hr. food deprivation with a 23-hr. water deprivation is the physiological equivalent of a combination with 0-hr. water deprivation. The facts of drive discrimination (Hull and Leeper) make such an assumption untenable.

Nevertheless, our results do not permit a final generalization along the lines of Muenzinger's theory until the problem has been further investigated with drives which are not as closely interrelated as hunger and thirst.

SUMMARY

The problem of this study was to find out whether the effect of combining two motives upon learning efficiency was greater than that of the motives used singly. On theoretical grounds we predicted that the combination would not produce such an effect.

Eighty hooded rats were divided into eight groups. Four of these were motivated by either hunger or thirst with two levels of deprivation, 6 hr. and 23 hr. Four groups were motivated by all possible combinations, namely, weak hunger and thirst, strong hunger and thirst, weak hunger and strong thirst, and strong hunger and weak thirst.

The learning situation was a Y-shaped discrimination box. The cues were black-positive and white-negative in a corrective method.

As predicted, four combinations of motives did not result in learning efficiencies that were greater than those of the better ones of the two motives taken alone.

In terms of trials to criterion the combination groups were poorer than the better one of the two single groups. In terms of errors the combination of weak hunger and thirst was likewise poorer than the better one of the single motives, while the other three combination groups were either the same or slightly and insignificantly better than the better ones of the singly motivated groups.

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THE EFFECT OF ACTIVITY DEPRIVATION UPON EXPLORATORY BEHAVIOR

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In previous papers (e.g., 3) the author has advanced the hypothesis that novel stimulation arouses the exploratory drive, which leads to exploratory behavior. A commonly accepted alternative hypothesis is that exploratory behavior is motivated by the "general activity drive," i.e., exploratory behavior is one form of "general activity."

Several lines of evidence suggest that the latter hypothesis is invalid. Anderson (1) found no significant correlations between one measure of general activity and several measures of exploratory behavior. The results of several experiments by the author (3, 4, 5) show that the amount of exploratory behavior of rats decreases rapidly during a 10-min. period of exposure to a simple maze and that it increases with size of maze. It seems unlikely both that the general activity drive decreases in strength this rapidly and that it is a function of maze size. The same studies reveal that exploratory behavior is largely under the control of, i.e., directed by, external stimulation, a finding difficult to explain in terms of the general activity drive alone. A related finding (5) is that the decrement in amount of exploratory behavior produced by exposure to one maze generalizes to other mazes, decreasing in magnitude as the similarity of the mazes decreases. Again, this is a fact difficult to account for on the basis of the general activity drive.

The present experiment is designed to answer this question: Does activity deprivation affect the amount, the relation to time, or the orderliness of the exploratory behavior of rats in a simple maze? It provides a direct test of the two hypotheses stated above. One operation that should increase the strength of the general activity drive is depriving normally nourished animals of activity. However, this operation should not affect the strength of the exploratory drive because the latter is aroused by external stimulation, not by factors internal to the organism. If the exploratory behavior of a group of activity-deprived animals is measured after various periods of deprivation and compared with that of a control group not so deprived, mutually incompatible predictions follow from the two hypotheses. (1) If exploratory behavior is motivated by the general activity drive, then as length of activity deprivation increases, exploratory behavior should (*a*) increase in amount during limited periods of exploration and (*b*) decrease in amount progressively less rapidly during successive periods of exploration. (2) If it is motivated by the exploratory drive, it should be relatively unaffected by activity deprivation either in amount or in its relation to time. No differential predictions about the order characteristics of exploratory behavior follow from these hypotheses.

METHOD

Subjects

The *S*s were 18 male albino rats of the Wistar strain. They were about 100 days old and experimentally naive. Prior to the experiment the animals were housed, 10 to a cage, in large living cages measuring 30 by 18 by 12 in.

Apparatus and Procedure

The rats were divided at random into two groups of nine each, a control group (C) and an experimental group (E). Over the eight-day experimental period each animal was housed in a small living cage, measuring 10 by 6 by 5 in., containing a food receptacle 3 by 3 by 3 in. All cages contained food and water at all times. For at least 22 hr. per day each rat in group C had free access to an activity wheel of a standard type measuring 14 in. in diameter by 4 in. wide. The animals in group E never had access to activity wheels.

Exploratory behavior was measured in an enclosed, symmetrical, single-unit Y maze constructed from unpainted white pine. Each arm was 24 in. long, 4 in. wide, and 4 in. high (inside dimensions), had a hinged hardware-cloth top, and was marked off into 12-in. sections. The maze was uniformly illuminated by dim indirect lighting.

Just before being placed in its small living cage for the first time, each rat was permitted to explore the maze freely for 5 min. (day 0). Twenty-four hours later (day 1), 72 hr. later (day 3), and 192 hr. later (day 8) each animal was exposed to the maze for 10 min. The rats were always placed in the maze at the choice point. Neither food nor water was ever present in the maze.

The data consist of (*a*) the number of activity-wheel revolutions per day for each animal in group C, (*b*) the number of 12-in. maze-section traversals for each animal during each minute of each maze exposure, and (*c*) the sequence of maze arms entered by each animal on each maze exposure.

After the maze exposure on day 8, four animals, matched on the basis of amount of exploratory behavior in the maze on day 8, were chosen from each group. These rats were kept in the small living cages for an additional ten days. Each animal was given free access to an activity wheel for 24 hr. per day. Daily activity records were taken. This procedure provides an additional test of the general-activity-drive hypothesis. From this hypothesis it follows that the animals from group E, after eight days of activity deprivation, should show an initial high level of activity exceeding that of the rats from the control group, followed by a decrease to the control-group level.

TABLE 1

Summary of the Activity-Wheel Data for Group C

PERIOD IN HOURS	MEAN
0–24	242.7
24–72	544.6
72–192	1905.2
0–192	2666.9

RESULTS

Activity-Wheel Data

Table 1 presents the average number of activity-wheel revolutions for group C during each relevant experimental period. It is clear that these animals were fairly active over the eight-day period. Several ran one-half mile or more on one or more days. A day-by-day analysis shows a gradual increase in activity over the experimental period.

Figure 1 summarizes the activity-wheel data for the eight animals selected from groups C and E. It is apparent that the eight days of activity deprivation imposed on the rats in group E did not result in an immediate (or even delayed) higher level of activity than that exhibited by group C, or even a higher level than that shown during the first eight days by the group C animals. The groups are too small for tests of significance. However, these data suggest that if activity deprivation exerts any effect, it is that of decreasing amount of behavior.

Amount of Exploratory Behavior

The number of 12-in. maze-section traversals per minute was tabulated for each animal on each maze exposure. These data are summarized in Figure 2, which shows average amount of exploratory behavior as a function of time for each group on each day. There are no apparent differences between groups on any day. The average total number of 12-in. maze-section traversals for groups C and E on days 0, 1, 3, and 8, respectively, are: 36.6, 44.1, 41.9, and 45.9; and 33.4, 42.7, 37.1, and 45.8. The respective means for all four days are 168.4 and 159.0. None of the differences between these means approaches significance. It is evident that increasing lengths of activity deprivation of the kind employed

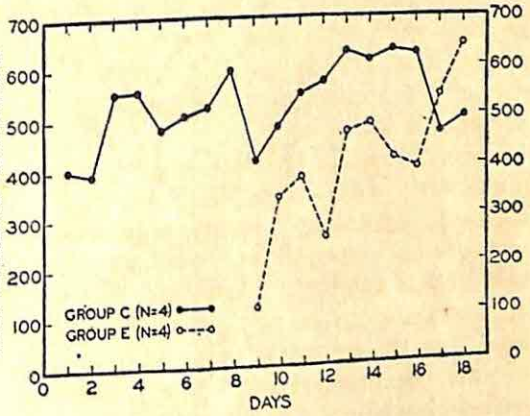

FIG. 1. Average amount of activity-wheel behavior as a function of days

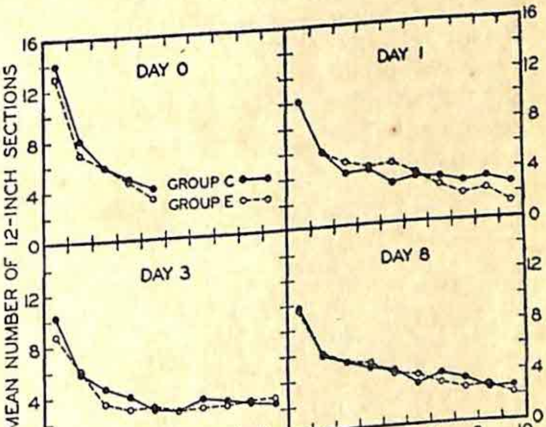

FIG. 2. Average amount of exploratory behavior as a function of time

in this experiment have no effect upon either the amount of exploratory behavior in a simple maze or its relation to time of exploration.

Orderliness of Exploratory Behavior

As in previous studies (e.g., 4, 5), a measure of the orderliness of exploratory behavior was obtained by (*a*) tabulating the number of times each animal entered three unlike maze arms in succession and the number of times it could have done so for each maze exposure, (*b*) summing both sets of values for each group, and (*c*) converting them into percentages. The results are summarized in Table 2. Inspection of the table reveals no differences between groups on any one day or on all days combined. The average percentage for both groups over all four days is 70.3, a value in close agreement with corresponding percentages found in previous studies (5, 6) in which female rats were used. In brief, activity deprivation of the kind employed in this experiment has no effect upon the orderliness of exploratory behavior in a simple maze.

TABLE 2
Per Cent Choice of Three Successive Unlike Arms On Each Day

DAY	GROUP C		GROUP E	
	*N**	%	*N*	%
0	75	74.3	59	67.8
1	85	69.1	93	69.4
3	84	68.8	70	68.0
8	102	71.8	93	72.7
Total	346	70.9	315	69.7

* *N* represents the total number of triads containing three unlike members.

It should also be mentioned that *E* detected no qualitative differences in the maze behavior of the animals in the two groups.

Correlational Data

Although the number of animals per group is relatively small, several rank-order correlation coefficients were computed. The test-retest rho (first three days vs. last five days) for the activity-wheel measures taken on group C is .88. The test-retest rho (days 0 and 1 vs. days 3 and 8) for amount of maze behavior for all 18 rats is .80. Both values are significant at the .01 level (2, pp. 46–49). The rho for total amount of activity in the drums over the first three days vs. the total amount of maze behavior on day 3 for group C is .81. The corresponding rho for the last five days in the drum vs. maze activity on day 8 is .10. The former value is significant at the .01 level; the latter does not differ from zero. In brief, both the activity wheel and the maze are fairly reliable measuring instruments, and the initially high correlation between drum and maze activity drops to zero during the latter part of the experimental period.

DISCUSSION AND CONCLUSIONS

The results of this experiment are unequivocal. They show that moderate activity deprivation over an eight-day period (*a*) has no effect upon the amount of exploratory behavior of rats in a simple maze, upon its relation to time of exploration, or upon its order characteristics, and (*b*) does not lead to an above normal amount of activity-wheel behavior. These findings are completely negative with respect to the hypothesis that exploratory behavior is motivated by the general activity drive. On the other hand, they support the author's hypothesis that the exploratory drive is a relatively independent primary drive aroused by novel external stimulation.

A possible criticism of the present experiment is that the animals in group E may have been as active, or nearly so, outside of the maze as those in group C. None of the author's observations supports this criticism. Every time *E* entered the room in which the animals were kept, the animals in group E were asleep, lying quietly, or otherwise inactive, whereas those in group C were generally "up and about." It was often necessary to take precautions to insure that the rats in group E would be awake and active for their maze exposures. Moreover, it is difficult to see how the animals in group E could have been nearly as active as those in the other group. The living cages were so small that the rats could barely turn around comfortably; on the other hand, the group C animals could (and frequently did) run back and forth between the activity wheels and their cages without actually turning the wheels.

The initial high correlation between amount of activity-wheel and maze behavior and its subsequent decrease to zero merit discussion. Each apparatus proved to be a fairly reliable measuring instrument; hence the explanation must be sought elsewhere. It seems likely that during the first two or three days the activity drums presented relatively novel stimuli to the animals in group C, as did the maze. Hence, both situations evoked exploratory behavior, and the correlation was high and positive. With repeated exposures the exploratory-drive-evoking power of the activity wheels decreased, other factors began to operate, and the correlation dropped to zero. The nature of these other factors is open to empirical investigation. However, the activity-wheel data suggest that some kind of learning or adaptation occurred: there was a gradual increase in average activity over the eight-day period for group C, and Figure 1 reveals a similar trend for both subgroups.

It should be noted that these data corroborate, rather than contradict, Anderson's (1) report of zero correlations between activity-wheel behavior and exploratory behavior. He kept his animals (male rats) in activity wheels for eight weeks, and used only the measures taken during the last four weeks in computing his correlations.

Two major conclusions are drawn from the results of this experiment. (*a*) Because prolonged moderate activity deprivation exerts no effect of any kind upon the exploratory behavior of rats in a simple maze, it is concluded that exploratory behavior is independent of the general activity drive. (*b*) For the same reason, and because of previous data (6), it is concluded that the exploratory drive is a relatively independent primary drive aroused by novel external stimulation. The data from the present study, especially those summarized in Figure 1, provide no support for the concept of the "general activity drive"—a modern version of the "excess energy theory." A further and a very tentative conclusion is that this concept may not be useful in the analysis of behavior.

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COLOR DISCRIMINATION IN THE BLUEGILL SUNFISH[1]

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The object of this experiment is to determine whether or not the bluegill sunfish (*Lepomis macrochirus*) can discriminate red from green.

Warner (9) presents a comprehensive review of the controversial literature concerning color vision in fish up to 1931. The weight of the evidence he cites favors discrimination, but in none of the experiments cited was the intensity variable completely controlled. As early as 1885 Graber (4) demonstrated that although fish appeared to show an innate preference for red over blue, the preference could be reversed by increasing the red to 20 times its former intensity. Hess's experiments (5) show that not only is light intensity an important source of variability in fish behavior, but that the curve of physiological intensity plotted against wave length is similar to that for humans with scotopic vision.

For the above reason, the studies of Washburn (10) and Reighard (7) are inconclusive. The above *E*, using learning techniques, taught fish to discriminate between colors whose intensities were, to the human eye, equal. They then varied intensity of the reinforced color and continued to get positive results. Goldsmith (3) used similar techniques of learning and intensity variation, but equated physical intensity by use of photographic plates instead of human judgment. Schiemenz (8) used a technique similar to Goldsmith's with 12 different intensities. However, in none of these studies was the original intensity-equating done by the fish, and Graber's factor of 20 shows the possible existence of very large differences between physiological intensities for equal physical intensities. Furthermore, Hess (6) reported that preference for red over yellow or white decoy larvae could also be obtained for varying shades of gray, although von Frisch (2) failed to confirm these results.

The foregoing studies seem to have been adequate to convince most people that color vision in the fish is a closed question, or else an unimportant one, as there is little mention of the subject in the literature since 1931. However, one study by Bull (1) deserves particular mention as it shows a somewhat closer approach to complete control of the intensity variable. The *S*s (*Blennius pholis L.*) were conditioned to differentiate those colors which were followed by electric shock from those which were not. Discrimination was obtained with separate groups of *S*s for ten different colors, while other *S*s of this species could be trained to discriminate only very wide differences in intensity between two grays. However, there is still the possibility that the physically equated colors were as different in physiological intensities as the two discriminated grays, great as this difference was, and that physiological intensity was the crucial cue.

One way to show that the observed color discriminations did not result from differences in physiological intensity would be to demonstrate that the *trained* *S*s—those that had already learned the color discrimination and were presumably reacting to wave length as the crucial cue—would not respond differentially to differences in intensity when the color was held constant. This is the purpose of the present experiment.

METHOD

In an earlier unpublished experiment by the author, the conditioning technique was employed to establish color preference in the bluegill sunfish. A food box was lowered into the aquarium in the presence of red or green light of a range of physical intensities between 1 and 45 ft-c. When the red light was on, the box contained angleworms; when the green light was on, it was empty. It was reasoned that if a preference could be demonstrated—the fish entering the box in the presence of red, refraining from entering in the presence of green—the intensity factor could be rigorously checked by substituting, for the red and green lights, white lights of widely varying intensities. It would be predicted that if the fish had learned their responses to wave-length differences, they would either respond randomly to the different intensities of white or else would not respond at all.

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[1] This experiment was conducted under the auspices of the department of psychology of the Pennsylvania State College.

Unfortunately, no conclusive results were obtained in this experiment. Once the *S*s had learned to respond, they responded almost invariably to both red and green. The difficulty was diagnosed as a failure to force the discrimination; there was no penalty for a response to green, the indifferent stimulus. The above experiment was reported because in the present inquiry (*a*) the same individuals were used as *S*s, and (*b*) similar apparatus was used, except that the latter was arranged in such a manner as to force the discrimination.

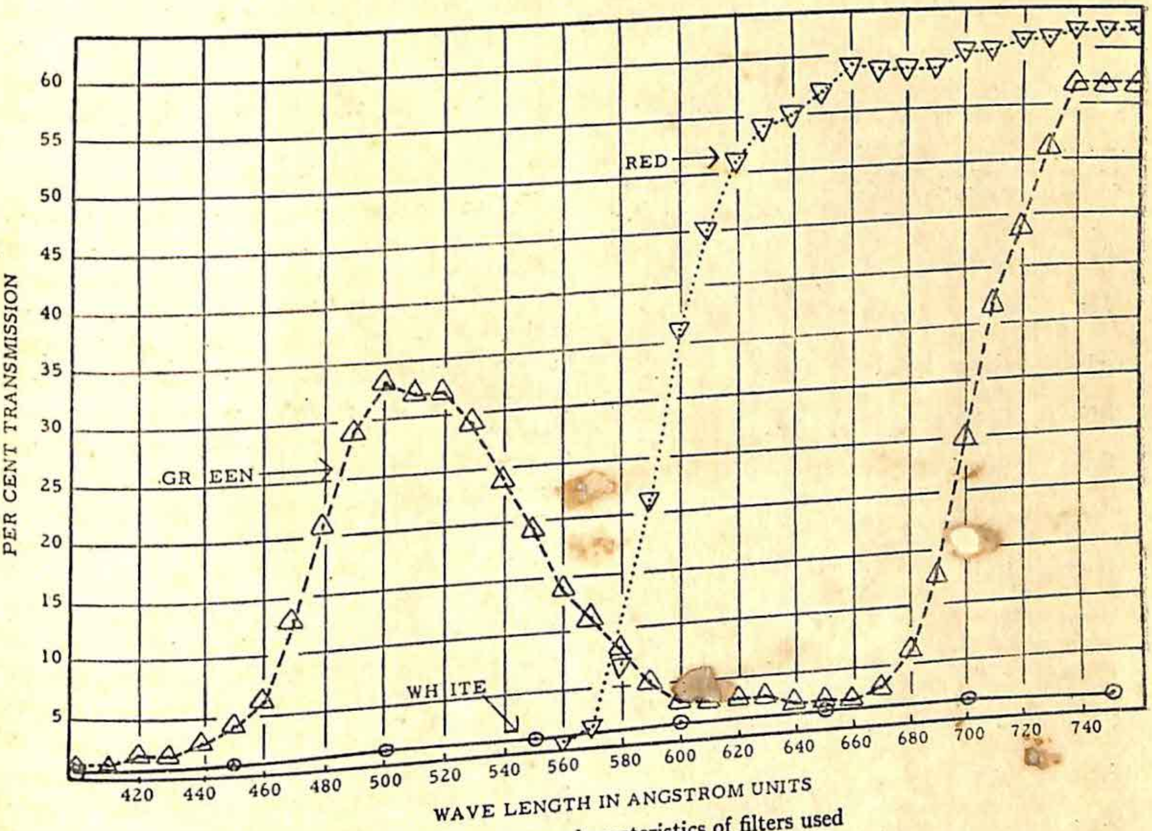

FIG. 1. Transmission characteristics of filters used

In the present study, four bluegill sunfish from 3 to 4 in. long, which had already received 100 trials in the previous experiment, were the *S*s. Differences in size and coloration permitted identification. They were kept in a 50-gal. glass aquarium during the course of both this and the previous experiment. Food boxes with top and one side open were used to present the food, which was pieces of angleworms. Red, green, and white light beams were presented by lantern slide projectors equipped with broad-band filters of colored cellophane. The transmission characteristics of the filters are mapped in Figure 1. The author recognizes the inadequacy of such filters for the mapping of color vision. However, since the purpose of this experiment is to establish color vision, not to map it, any technique which permits wave length to be the sole variable could be adequate even though we do not know the exact wave lengths responded to.

In order to force the discrimination, a food box was placed at each end of the aquarium. The two lantern slide projectors rigged to spotlight the food boxes were connected to separate current sources, one of which had the rheostat used in the previous experiment set to give beams of 1-, 15-, 30-, and 45-ft-c intensity, varied randomly. The other always projected a beam of 45-ft-c intensity. The filters were changed between projectors 1 and 2 (hence also between food boxes 1 and 2) in a random manner, so that sometimes the red was at the right and as much as 45 times the physical intensity of the green, and sometimes the green was at the right and as much as 45 times the physical intensity of the red. Physical intensities were measured with a Weston foot-candle meter. Beginning with trial 14 of this experiment (learning trial 114 for these *S*s) similar white filters were placed on both projectors simultaneously for approximately 1 trial out of 4 (randomized). This was to be the ultimate check on the intensity variable, as described in connection with the previous experiment.

Both food boxes were left in the aquarium all the time, and anticipatory responses were used as the criteria for choice. Thus, in a typical red and green trial, the room was darkened and both food boxes were illuminated simultaneously, one with red light and the other with green light. Five seconds after any fish entered either box (any part of the fish's body entering the box being counted a response), the colored lights were extinguished. However, if the response was to the red-illuminated box, the respondent was fed a piece of angleworm before the lights were extinguished. This was accomplished by having *E*, who stayed in a specified position between the boxes, give the worm to the fish by hand. *E* did not himself move until the response to be tabulated had been made. In a typical noncolor or check trial, in which the white filters were employed, the lights were manipulated in the same manner except that it was recorded whether the fish responded to the more or to the less intense of the two stimuli. Neither was reinforced.

TABLE 1

Choice Responses under the Various Conditions

COLOR OF VARIED INTENSITY	COLOR OF CONSTANT INTENSITY	INTENSITY OF VARIED COLOR (FOOT-CANDLES)	COLOR OR INTENSITY CHOSEN	TOTAL RESPONSES (ALL SUBJECTS)
Red	Green	1	Red	11
			Green	3
Red	Green	15	Red	12
			Green	0
Red	Green	30	Red	12
			Green	0
Red	Green	45	Red	13
			Green	1
Green	Red	1	Red	9
			Green	1
Green	Red	15	Red	8
			Green	1
Green	Red	30	Red	11
			Green	1
Green	Red	45	Red	17
			Green	0
White	White	1	Bright	6
			Dim	3
White	White	15	Bright	2
			Dim	4
White	White	30	Bright	3
			Dim	8
White	White	45	Bright	1
			Dim	1

It is to be noted that only one response, the first, was recorded in each trial, so that each trial was independent of the next with regard to intensity and the relative positions of the red and green. Thus, social factors were controlled in the four fish. By using the anticipatory response technique, all cues resulting from presence or nonpresence of the food were eliminated. If the fish responded differentially to the red and green, but not to the two whites, it could be inferred that they were responding to differences in wave length.

RESULTS

As indicated in Table 1, in a total of 101 responses made by the four fish during red-green test trials, 94 were to red and 7 to green.

Each individual fish showed this trend, the highest ratio of green to red chosen by any one of them being 2 to 15. The lowest ratio of green to red chosen was 1 to 34.

In the noncolor trials there were 12 responses to the more intense of the two white stimuli and 16 responses to the less intense, with 2 failures to respond at all.

By chi-square technique, results for total red vs. green preference were significant well beyond the .001 level, while results for intensity preference in the noncolor trials were between the .50 and .30 levels of significance.

DISCUSSION

The results on the total red vs. green responses were unequivocal—the *S*s did react preferentially to the red, beginning apparently with the first trial of the experiment. In the author's previous experiment considerable learning seems to have taken place which was not manifest in performance until the design was changed. This emphasizes the need for forcing the discrimination in such experiments instead of relying on the "law of least effort."

The check on intensity by the white vs. white choice failed to disprove the null hypothesis—i.e., that the fish were not reacting differentially to intensity. While such negative proof cannot absolutely rule out intensity as a source of variability in this experiment, it certainly does show that intensity alone is insufficient to account for the huge preponderance of red over green choices, especially since the greatest percentage of green choices occurred when the green was 45 times the physical intensity of the red.

In view of the facts that the *S*s did respond differentially to the red and green and that the difference could not be explained on the basis of extraneous cues, we must conclude that *L. macrochirus* can discriminate differences in wave length.

SUMMARY

Four specimens of *L. macrochirus*, the common bluegill sunfish, were conditioned to receive food at a red-illuminated box and no food at a green-illuminated box. Color of illumination was varied randomly from one box to the other, both being illuminated simultaneously so that the fish had to choose which one to enter. Intensity was varied randomly.

Anticipatory responses were used as the criterion of choice, and only the first fish to respond was tabulated. Approximately one trial in every four (determined randomly) took place with two white lights of varying intensity substituted for the red light and the green light. The *S*s showed a strong preference for red over green after having been conditioned, but the choices of greater or lesser white intensity, made under the same conditions as the color choices, were nearly equal. It was concluded that an explanation of the differences in responses to red and green must invoke the wave length as a necessary cue.

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ULTRASONIC HEARING IN THE PORPOISE, *TURSIOPS TRUNCATUS*[1]

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Many of the mammals are known to respond to auditory vibrations in the ultrasonic or supersonic range, that is, above approximately 20,000 cycles/sec, the upper limit of hearing in man. The dog, for instance, can hear to 35,000 cycles/sec (2) and cats to 40,000 or 50,000 cycles/sec (2, 3), while mice and bats have upper frequency thresholds as high as 95,000 and 98,000 cycles/sec, respectively (1, 7). The mammals of the sea seem to have been studied hardly at all in this respect, yet there is good reason to believe that at least some of them possess unusual acoustic abilities.

What of the whales and porpoises, for example, which are known to produce many sorts of noises? Since even in the clearest ocean water the visibility for objects at a distance is but a small fraction of what it is in the air, the probabilities are that these organisms use some form of echo-ranging or echolocation to orient themselves in their environment, as bats do in the air (4, 10). If this were not the case, it is hard to imagine by what method they avoid colliding with the bottom or with submerged objects, especially when swimming at night, at great depths, or at a high rate of speed.

If they do respond to the reflected echoes of their own noises, this implies in turn a sensitivity to auditory vibrations in water which must be very acute indeed. In some species, this sensitivity may well extend into the ultrasonic range. Porpoises or dolphins have in fact, been seen to swim rapidly away from a vessel at the sound of a supersonic depth finder (5), an observation which clearly implies that they heard the sounds produced.

The present article gives new and more extensive evidence on high-frequency hearing in some of these cetaceans, with specific reference to the bottle-nose dolphin or porpoise *Tursiops truncatus* (Montagu).

METHOD

Obvious difficulties present themselves when large animals, immersed in water, are to be studied. Even though they are captive specimens in tanks or enclosures, they can hardly be thought of, or treated, like laboratory animals. They cannot—or have not yet—been placed within sound-insulated or non-reflecting chambers. And their movements in the water, which are generally uncontrollable, constantly alter their distance from the sound-producing apparatus. As a result of these limitations, it is doubtful if precise threshold measurements, in the usual sense of the word, can be obtained from behavior studies of the porpoise. Intensity thresholds are out of the question altogether, by any method except the measurement of cochlear potentials, although some approximation at an upper frequency threshold can be inferred from the study of behavior. The results obtained under conditions such as these should perhaps be considered as belonging closer to the category of "field" or "naturalistic" observations than to more exact laboratory findings.

Subjects and Testing Environment

Thirteen bottle-nose porpoises or dolphins, *T. truncatus*, were used in the present research. They were tested at three separate places, two of which were in Florida and one in the Bahama Islands, British West Indies.

Ten of the animals were observed at the Marine Studios at Marineland, Florida, where they were kept together in a large circular steel tank 12 ft. deep and 75 ft. in diameter. In the tank with them were two spotted or long-snouted dolphins (*Stennella plagiodon*) and several loggerhead turtles (*Caretta caretta*). The water was filtered, permitting easy visibility through windows in the walls of the tank below the surface, for the full diameter of 75 ft. All observations at Marineland were made through these windows below the water line.[2]

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[1] Contribution No. 14 from the Oceanographic Institute of Florida State University. This paper is a follow-up of a preliminary announcement which appeared in *Science* over a year ago (10).

The research was sponsored in part by the Office of Naval Research, the American Museum of Natural History, and the Research Council of Florida State University. Grateful acknowledgement is made to Mr. F. G. Wood, Jr., of the Marine Studios of Marineland, Florida, to Dr. P. S. Sperber, of the Daytona Sea Zoo, and to Dr. C. M. Breder, Jr., of the American Museum of Natural History, for permission to use the facilities under their control. We are also indebted to Dr. Harold J. Humm, Director of the Oceanographic Institute of Florida State University, for continued encouragement and support in these studies, and to Mr. Robert Kohler, the Institute's electronics engineer.

[2] So far as could be determined, the reactions of the long-snouted dolphins to the underwater sounds which

Two further specimens of *T. truncatus* were examined at the Lerner Marine Laboratory at Bimini, B. W. I., a field station of the American Museum of Natural History. Here they were kept together in an outdoor wire enclosure about 30 ft. by 50 ft. in the open water. The depth of the water in the Bimini enclosure was about 7 ft. at low tide and 10 ft. at high tide. The bottom was of white coral sand, and the water was naturally clear. Observers stood above the surface upon a pier or dock at the edge of the enclosure.

The thirteenth animal was a trained specimen, which had been in captivity for about two years. It was examined alone in an excavated pen or pool at the Daytona Sea Zoo, Daytona Beach, Florida. The pen was a part of a long canal about 40 ft. wide and 8 to 10 ft. deep, into which brackish tidal water flowed. Both ends of the pen, which was about 60 ft. long, were of wire fencing, and the bottom was soft sand, with some mud. Although fairly free from sediment, the water was a clear brown color, with visibility not exceeding 1 or 2 ft. The dolphin could therefore not be seen when it was submerged. Nevertheless, the observations of this animal were in some ways more significant than any of the others, since they afforded the opportunity for studying a single individual in isolation, uninfluenced by the activity of other organisms.

The ages of the two females at the Bimini Laboratory were estimated to be about four years. Most of the animals at Marineland (including both sexes) were older, as judged by their size and weight. The age of the Daytona specimen was unknown, although it was mature. Probably it was a female.

Apparatus

The sound-producing gear consisted of a Hewlett-Packard Model 200C oscillator, capable of transmitting sine waves of from 20 to 200,000 cycles/sec. The signal of the oscillator was fed through a 20-w. amplifier whose output was essentially linear to 100,000 cycles/sec into a USRL-type 1K underwater speaker or transducer loaned by the United States Navy on ONR contract. The transducer was capable of emitting frequencies at least to 200,000 cycles/sec (200 kc.), although at reduced and variable intensities beyond 10,000 cycles/sec (10 kc.). The system as a whole was consequently uncalibrated for intensities.

However, the accurate transmission of the different frequencies, even though at varying intensities, was carefully checked in underwater sound tests, by the use of a special hydrophone and sound pick-up apparatus, recording through an oscilloscope. The signal for a given frequency would first be sent directly to the cathode ray tube of the oscilloscope, by-passing the underwater gear entirely. The same signal would then be projected and picked up under water, and again observed on the tube of the oscilloscope. A comparison of the direct and underwater signals on the screen of the cathode ray tube showed that the wave form was transmitted through water without distortion for the entire frequency range up to 200 kc.

Method of Testing

Since the porpoise is known to be wary of strange objects placed near it in the water, an opportunity was given in most of the tests for the animals to familiarize themselves with the visual appearance of the transducer before any sounds were projected. At Marineland an exact wooden replica of the transducer was intermittently lowered into the water during a period of about two weeks prior to the actual sound tests. At the Lerner Laboratory, although the wooden model was not available, the original speaker was allowed to remain in the porpoise enclosure for long periods (and overnight) when not in use. Because of the low degree of visibility of the water at Daytona Beach it was not deemed necessary to employ this method at that place.

In the tests themselves, the animals were stimulated by pure tones, in short bursts or beeps 1 to 3 sec. in duration, sent through the water by means of the transducer. The frequencies of these tones were randomly varied between 100 cycles/sec and 200,000 cycles/sec. Clicks and other on-and-off artifacts were avoided by the elimination of make-and-break switches altogether. Each stimulus was begun and ended by a volume control and so had a gradual onset and termination. The interval between successive stimuli extended from 30 sec. to several minutes in length. The development of adaptation to repeated sound stimuli was discouraged and retarded by interspersing the different sessions with long rest periods and by limiting the length of each session. From two to four observers were constantly on hand watching the animals whenever any sound tests were made.

RESULTS

Whether a particular stimulus was "heard" or reacted to was at once apparent from the nature of the swimming behavior which occurred. These cetaceans will avoid unusual sounds made in water. In most instances the response appears to be a kind of startle or flight reaction. The speed and rhythm of the swimming movements made by the trunk and tail flukes abruptly increase, and an entirely different "gait" or rate of locomotion is immediately assumed. If swimming space permits, captive porpoises will usually (although not always) dash rapidly away from the source of the sound. If there is no opportunity for avoidance or escape, they will suddenly swim faster in the original or in some different direction—in a kind of disturbed or "emo-

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were transmitted were the same as those of the bottle-nose dolphins. Yet, since only two of the former were available, the results reported here had best be considered as applying only to the bottle-nose dolphin, *T. truncatus*.

The turtles made no responses whatever to any of the acoustic stimuli.

tional" response pattern. The change in behavior is perfectly obvious and is not at all difficult to see. What is taking place is clear even to the uninitiated.

Tests at Marineland

To use this basic behavior pattern as an indication of acoustic sensitivity, the swimming before and after each beep or burst of sound was directly compared. In the first series of tests conducted at Marineland, accelerated swimming responses of this sort were consistently and uniformly produced by all frequencies between 100 cycles/sec and 50,000 cycles/sec. Considerable attention was given to the higher frequencies, and there can be little question about this finding. Since responses occurred regularly to the 50-kc. stimulus, this figure, if taken as a threshold reading, should be regarded as the highest 100 per cent point. Frequencies higher than this were not consistently reacted to. No attempt was made to explore the lower threshold for pitch, and no sounds below 100 cycles/sec were transmitted.

It was noted in the first observations at Marineland that the speed-up in swimming was not easy to obtain between 100 and 400 cycles/sec. In order to get a reaction within this frequency range, it was necessary to raise the gain or output of the apparatus by a considerable amount. When the volume was increased in this way and responses occurred, the nature of these reactions for frequencies between 100 and 400 cycles/sec was often more violent and disturbed than that produced by the other frequencies. The animals sometimes dived out of the water, and occasionally made swerving "attacks" or "charges" in the direction of the transducer, instead of swimming away from it. A human evaluation of such behavior might characterize it as "anger" rather than "fear."

This result was obtained only in the circular tank at Marineland, and never in the later determinations at Bimini or at Daytona. The effect is to be attributed, we think, to the high level of background water noise existing in the steel tank at Marineland—a noise level which was itself of low frequency. The increasing of the energy of the stimuli sufficiently to break through this masking or interference may also have resulted in stimulating the tactual receptors of the animals. In such cases they would have "felt" the vibrations on the skin. At any rate this phenomenon was entirely absent in the quiet water at the Lerner Laboratory and at Daytona Beach, and at these places no qualitative difference was observed in the nature of the responses given to any stimulus, no matter what its vibration rate.

Tests at Bimini

In the second series of tests upon the two young animals at the Lerner Laboratory, the usual flight responses occurred regularly to vibrations as high as 80,000 cycles/sec (80 kc.). The observation was again carefully checked and rechecked, and we are confident that there can be no error in this approximate threshold level. The figure of 80 kc. is again a 100 per cent value, not a 50 per cent or 75 per cent threshold point.

The difference between the two results of 50,000 and 80,000 cycles/sec may be due in part to the youthfulness of the porpoises at Bimini, since the upper limit of hearing is known to decrease in many organisms with age. Perhaps a more satisfactory interpretation, and the one which now seems to us to be the correct one, would explain the discrepancy in terms of the varying conditions under which the two sets of tests were conducted. The difference is again traceable, we think, to the high noise level in the steel tank at Marineland. Sounds of pumping water, of drainage, of water currents, and of splashing were continuous. At Bimini, on the other hand, since tidal water flowed freely through the wire fencing of the outdoor enclosure, no pumping or drainage was necessary. As a result, the noise level of the water was much lower. Quite likely, therefore, it was the interference caused by uncontrolled water noise which produced the lower reading in the first instance.

Tests at Daytona Beach

A final check made with the isolated dolphin which was tested at Daytona generally confirmed the earlier findings. Since the Daytona animal was tame and had been in captivity a long time, it spent a good deal of time floating (without swimming) at the top of the water, ogling the humans on land first with one eye and then the other. But as soon as the transducer had been lowered into the water, the porpoise submerged and began a slow and deliberate swimming about the enclosure, mostly at the end farthest from the instrument. Because of the opacity of the water, the location of the animal could not always be determined except when it came up for air.

Such conditions did not appear at first to favor the observation of any behavior changes. Yet it soon became apparent that whenever a sound was projected into the water, the position of the animal, its speed, and its direction of motion could be determined. These were indicated by the tell-tale V-shaped wake which immediately appeared upon the surface. The wake was not produced by the ordinary slow swimming in which the porpoise indulged when not responding to acoustic stimulation. It was caused only when the speed of swimming was increased by the typical avoidance or startle response, which now became observable in this indirect manner.

The use of this cue to the change in swimming speed permitted the corroboration of the previous findings at Marineland and Bimini, although to slightly different limits. The Daytona Beach porpoise reacted without fail to all frequencies up to 50,000 cycles/sec, and 75 per cent of the time to frequencies of 60,000 cycles/sec, but the results were doubtful or negative at 70 kc. and above. Two possibilities suggest themselves as to why responses were not obtained at higher levels, when they did occur regularly at Bimini to stimuli of 70 and 80 kc.: (*a*) The soft character of the bottom at Daytona undoubtedly affected sound transmission at these threshold frequencies by absorbing a greater portion of the sound energy than at Bimini, and (*b*) individual differences between the *S*s tested.

The order or position in which these findings place the bottle-nose dolphin with regard to acoustic sensitivity, in comparison with other organisms, can be seen from Table 1. The first column in the table gives the ranking or order of the organisms listed in terms of the number of vibrations/sec (as shown in the third column) to which it has been observed to respond. The investigator, or investigators, reporting these results are shown in the fourth column. It will be noted that if the maximum finding of 80,000 cycles/sec is taken, the porpoise is exceeded by only two other animals in its responsiveness to high-frequency tones. One of these animals (the bat) is known to *emit* or *produce* sounds of very high frequency also, which it uses for the purpose of echo-ranging or echolocation while in flight (7).

This unusual ability of the bottle-nose dolphin to respond to high-frequency vibrations in water receives additional support in the structure of the auditory receptor and the acoustic centers of the brain and might well have been predicted from their anatomy. Thus the ears of both whales and porpoises have a large earbone or bulla attached directly to the ossicles (8, 9). This structure, which takes the place of the tympanic membrane in air-dwelling mammals, is especially adapted to the reception of vibrations in a medium as dense as water. Moreover, the enlargement of the auditory centers in the temporal lobes in *T. truncatus* is tremendous, producing an over-all cerebral development which makes the hemispheres wider than they are long. Remington Kellogg writes of the bottle-nose dolphin as follows: "... these porpoises have a highly developed central nervous system for the reception and disposal of cochlear stimuli, which stands out in contrast to the less well developed optic mechanism. The optic colliculus was found to be not more than

TABLE 1

Rank or Order of Certain Organisms According to Upper Frequency Threshold

RANK	ORGANISM	UPPER THRESHOLD	INVESTIGATOR
1–3	Frog	10,000	Yerkes
1–3	Canary	10,000	Brand & P. P. Kellogg
1–3	Pigeon	10,000	Wever
4	Human (adult)	20,000	Fletcher
5	Human (child)	23,000	Elder
6	Chimpanzee	26,000	Elder
7	Dog	35,000	Dworkin
8	White rat	40,000	Gould & Morgan
9	Cricket	45,000	Wever & Bray
10	Cat	50,000	Dworkin
11	Porpoise	80,000	W. N. Kellogg & Kohler
12	Mouse	95,000	Dice & Bartow
13	Bat	98,000	Galambos

one-fourth as large as the acoustic colliculus" (9, p. 204).

SUMMARY

Using special underwater sound gear, in part loaned by the United States Navy on ONR contract, 13 captive porpoises or dolphins, *Tursiops truncatus*, were tested for their reactions to short bursts of sound between 100 cycles/sec and 200,000 cycles/sec. The responses made to such stimuli consisted in the main of flight or avoidance behavior which expressed itself as a rapid increase in the rate of swimming.

1. In one group of ten animals at the Marine Studios at Marineland, Florida, reactions of this sort were uniformly obtained to all frequencies between 100 cycles/sec and 50,000 cycles/sec.

2. In another group of two animals at the Lerner Marine Laboratory at Bimini, B.W.I., responses occurred regularly to frequencies between 100 cycles/sec and 80,000 cycles/sec.

3. In a third series of tests conducted with a single porpoise at the Daytona Sea Zoo in Daytona Beach, Florida, responses occurred on all trials at 50,000 cycles/sec and 75 per cent of the time at 60,000 cycles/sec.

4. The variation between these three sets of figures is attributed to the more favorable conditions (less background noise) obtaining at Bimini, to bottom conditions (more sound absorption) at Daytona Beach, and to individual differences among the animals tested.

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THE DIFFERENTIAL EFFECT OF A ROTARY VISUAL FIELD ON SUSCEPTIBLES AND NONSUSCEPTIBLES TO MOTION SICKNESS[1]

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Most studies reporting symptoms of motion sickness resulting from various visual stimuli indicate that angular displacement of the visual field is the most effective stimulus.

This displacement of the visual field has usually been accomplished in two ways. It may be an entire room which either oscillates about a horizontal axis from which the *S* is suspended in a swing (7, 9), or tips right and left about a horizontal axis with a stationary *S* (8). A second method is to have *S* fixed and to rotate around him a cylinder, the inside of which is painted with vertical stripes (2, 3, 6). These conditions impart an apparent motion of the body, and some *S*s experience nausea. Those stimuli which revolve about a vertical axis result in optokinetic nystagmus, to which Vogel (6) related the occurrence of nausea and dizziness at a critical frequency of 12 rpm. At this particular frequency, with his apparatus, he recorded the most regular nystagmus. At higher and lower frequencies, he found either irregular or no nystagmus and none of the motion sickness symptoms.

There is some doubt as to whether a vigorous horizontal optokinetic nystagmus is a necessary condition for the development of motion sickness symptoms, though, perhaps, visual attention and probably some attempt at fixation are required. Such a nystagmus was not present in the situation described by Wood (9), wherein the visual field did not rotate but merely oscillated about a horizontal axis which was lateral to *S*. In Witkin's situation (8), nystagmus was also not a factor. Here, relatively slow tipping movements of the room about a horizontal axis medial to the stationary *S* brought about nausea. Interestingly enough, the nausea was alleviated by the introduction of simultaneous movement of the *S* and the room.

Apparently, mere optokinetic nystagmus and apparent body movement are not sufficient to arouse nausea. Lebensohn (5) could not inhibit gastric activity with just the small surface of a kymograph drum, though apparent motion and nystagmus were present. Colley (3), however, utilizing a cylinder rotating about the whole body, found inhibition of contractions and an atonic condition of the stomach by roentgenological examination. His description of the alteration in gastric activity coincides with Hatcher's (4) as to the sequence of events at the commencement of nausea and vomiting. It is apparent that an adequate visual stimulus for nausea requires a relatively large, moving visual area.

In most such experiments it was customary to find that only a few *S*s became nauseated. The purpose of this investigation was to determine if these individual differences in susceptibility to nausea induced by visual stimulation could be related to individual differences in susceptibility to motion sickness.

METHOD

Subjects

The motion sickness questionnaire utilized and validated by the Wesleyan studies (1) was used as a basis for the selection of *S*s. Seven women and 9 men were chosen for the susceptible group (scores 24 and below), and 5 women and 14 men for the nonsusceptible group (a score of 38). All *S*s were students attending the summer session.

Apparatus

A room 8 ft. square with 70 in. high walls of fiber board and a ceiling of stretched burlap was constructed. The cream-colored interior was unpainted. The entire room was centered on a revolving horizontal wheel, 42 in. in diameter, driven by a ⅓-h.p. motor. A Variac, type 200-CU, manufactured by the General Radio Company, was introduced into the motor circuit to adjust the angular velocity. The velocity could also be varied by means of a lever which changed the tension of the belt which drove the base wheel. The angular velocity could thus be varied from zero to 24 rpm. The *S*'s chair was in the exact center of the room, supported by a pipe which extended from the bottom of the chair seat down through the wheel bearing to the wheel base. A second pipe extended from the top of the chair frame up through the ceiling of the revolving room and was anchored to the rafters of the experimental room. The chair was completely independent of the rotating room and remained stationary when the room revolved. It was possible, however, to revolve the chair by hand when standing in the room. For illumination, a 60-w. bulb was placed on the forward edge of the upper framework of the chair.

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[1] From a thesis submitted to the graduate school of the State College of Washington in partial fulfillment of the requirements for the Degree of Master of Science.

[2] Now at Army Medical Service Graduate School, Walter Reed Army Medical Center, Washington, D. C.

Procedure

After being seated, the *S*s were instructed to keep their eyes open and watch the floor, walls, and ceiling of the room, rather than some part of their body. If they felt they were going to vomit, they were to instruct *E* to stop. The *S*s were not told the chair would revolve, but after they were in the chair, it was spun around once to give the suggestion that they, and not the room, would be spinning. The program of velocities was to accelerate the room during 14 sec. to 24 rpm and maintain a period of constant velocity for 20 sec., and then switch off the current and allow the room to decelerate for 20 sec. to a velocity of 9 rpm. The cycle was immediately repeated and continued for 10 min., or until *S* requested rotation to stop.

RESULTS AND DISCUSSION

The resulting symptoms were the basis for categorizing *S*s:

a. Nausea. Those *S*s who requested the motion to stop before the 10-min. period was completed, and those *S*s who by their own reports indicated they were just able to last out the full 10 min. This group was typified by having to rest before leaving the experimental room, and by their fear of immediate vomiting.

b. Light nausea. These *S*s lasted out the full 10 min., but upon being questioned afterwards reported "feelings" of nausea. They expressed the belief that they would have vomited if they had been exposed for a longer period of time.

c. Dizziness. This group reported dizziness after stimulation, but no nausea.

d. No nausea and no dizziness.

The results are presented in Table 1. When questionable, all judgments were made conservatively, that is, in the direction of lesser nausea. Most, though not all, judgments were made without the knowledge of the susceptibility group in which *S* fell.

Of the four *S*s classified in the "nausea" category, three requested that rotation be stopped before the 10-min. period had elapsed. Two men lasted for 2½ and 5½ min., respectively, while one woman requested rotation to stop after 7½ min. No decided sex differences in the occurrence of nausea were noted.

TABLE 1

Incidence of Nausea in Relation to Susceptibility

GROUP	*N*	NAUSEA	LIGHT NAUSEA	DIZZINESS	NO NAUSEA
Susceptibles					
Male	9	3	3	2	1
Female	7	1	2	3	1
Both sexes	16	4	5	5	2
Nonsusceptibles					
Male	14	0	0	6	8
Female	5	0	0	1	4
Both sexes	19	0	0	7	12

TABLE 2

Incidence of Nausea in Relation to Perceived Rotation

PERCEIVED ROTATION	NAUSEA	NO NAUSEA	ALL GROUPS
Positive chair was revolving	1	14	15
Thought chair was revolving	4	9	13
Thought room was revolving	2	3	5
Positive room was revolving	2	0	2
All groups	9	26	35

An inspection of the results reveals very clearly that individuals susceptible to motion sickness are also susceptible to nausea in a rotary visual field, and, conversely, nonsusceptibles are resistant. By grouping the data of Table 1 into four cells, using susceptibles and nonsusceptibles as the first and second classifications, symptom categories *a* and *b* as the third, and categories *c* and *d* as the fourth, a fourfold table results. The null hypothesis that such a distribution of individuals arose by chance is refuted by a probability value of .012 as indicated by chi square computed by the direct method. It may be concluded that some of the individual differences found in previous studies may be related to the *S*s' motion sickness susceptibility.

Informal discussion with several of the *S*s a few days afterward indicates that the effects of this particular form of stimulation may last for some time. One of the nonsusceptible men reported only dizziness immediately following stimulation, but after he left the experimental room he began to feel slightly nauseated. This condition lasted for about 2 hr. The *S*s were categorized in terms of the reports immediately following rotation, and no changes were made on the basis of any later information. One susceptible man in the "light nausea" category lost his appetite for lunch. A susceptible man in the "nausea" category, who requested rotation to stop after 2½ min., vomited upon reaching home and complained of aftereffects consisting of a severe headache and light nausea for the following two days. These aftereffects were particularly noticeable when he was watching large, moving objects.

The *S*s' reports as to whether the room (true motion) or the chair (apparent motion) was actually revolving are of interest. Table 2 presents these data in terms of those *S*s who fell into symptom categories *a* and *b* (nausea group), and those *S*s who fell into symptom categories *c* and *d* (no-nausea group). Thirty-three *S*s were ignorant of the structural features of the equipment and were subjected only to the *E*'s indirect suggestion that the chair would be turning. Two *S*s knew the true nature of the equipment; one (a susceptible) was classified as "light nausea," and the other (a nonsusceptible) as "dizziness." Both *S*s reported that the chair seemed to be revolving in spite of their previous knowledge to the contrary. In the breakdown in Table 2, these two *S*s were arbitrarily placed in the "thought chair was revolving" category.

For those *S*s who thought that either the chair or the room could be revolving and were not positive as to the true state of affairs, the illusion of rotation would shift from room to the chair and back. For some, this alternation would occur without conscious effort. Other *S*s within this group found they could alternate the illusion voluntarily by watching some part of their body, or momentarily closing their eyes, even though they were specifically instructed not to do so.

From an inspection of Table 2 it is suggested that the individuals who perceived the apparent rotation tended to be unaffected, and, conversely, those who perceived the actual motion tended to experience nausea. The *N*'s involved in each cell are too small to permit adequate analysis, and further work is needed to determine if such a relationship is a true one.

SUMMARY AND CONCLUSIONS

1. Two groups of *S*s, one susceptible and the other not susceptible to motion sickness, were subjected to a rotating room situation in which they remained stationary. The resulting nausea symptoms were categorized on an arbitrary four-point scale.

2. The results indicate that individuals susceptible to motion sickness are also susceptible to nausea in a rotary visual field situation, and, conversely, nonsusceptibles are resistant.

3. It is concluded that some of the individual differences in regard to nausea found in previous studies utilizing rotary visual fields may be related to the motion sickness susceptibility of the subjects.

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AUTONOMIC BALANCE AND TEMPERAMENT[1]

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Several studies of autonomic balance, especially those of Darling (2), Darling and Darrow (3), Wenger (14, 15), and Wenger and Ellington (16), have been offered in support of the concepts of vagotonia and sympathicotonia, which were proposed earlier by Eppinger and Hess (4). A problem of further interest is the nature of possible relationships between autonomic balance and the emotional aspects of behavior which comprise temperament. The present study is an attempt to describe, by means of factor analysis, the order underlying a set of related measures of resting-level activity and of change in the autonomic nervous system, with a view to determining the structure of independent constitutional factors which may be associated with individual differences in traits of temperament.

An assumption which underlies previous factorial studies (2, 14, 15) is that either division of the autonomic nervous system can respond as a whole, and that the conditions of balance and imbalance are generalized and widespread, so that they involve simultaneous changes in a large number of organs and systems. The studies of Darling (2) and Wenger (14, 15), however, do not clearly support this assumption, since they include very few measures of autonomic change. More recent studies by Lacey and associates (8, 9, 10), on patterns of autonomic response, furnish strong evidence that the divisions of the autonomic system do not respond as a whole in normal individuals. Their results support a concept of autonomic response specificity in place of the concept of generalized autonomic reactivity. Such an interpretation appears to be adequately supported by the anatomical and neurochemical provision for restricted and localized responses in the parasympathetic nervous system.

It is proposed in the present investigation to increase the number of measurements of autonomic change, since it would appear that the most adequate test of autonomic balance should involve measurements of simultaneously changing functions. It is expected, too, that traits of temperament or emotional responsiveness may be more closely related to factors involving autonomic change than to factors mainly involving resting-level functions.

The hypothesis to be tested, then, is this: Between sets of scores in autonomic reactivity weighted with appropriate factor loadings and sets of scores in traits of temperament there will be significant correlations. The concept of generalized autonomic balance will be regarded as supported if several autonomic functions change together and load on common factors, either in the direction of sympathetic predominance or in the direction of parasympathetic predominance. On the other hand, if the autonomic functions vary independently and load on factors representing separate organs and systems, the concept of specialized autonomic balance will be regarded as supported.

METHOD

By means of a health data sheet prepared for this study by Dr. D. W. Terry, of Georgetown University Hospital, 100 ostensibly normal, male, white college students without known pathological involvements of the autonomic nervous system were selected for testing. The age range of the group was from 19 to 43 years. Care was taken not to test any individual sooner than 1 hr. after he had eaten or after he had engaged in strenuous exercise. Each *S* was allowed to relax for about 20 min. after arriving at the testing laboratory, so as to permit the recovery of normal blood pressure and heart rate before the test. The testing time for each individual was about ½ hr.

Experimental Design

By means of the simultaneous operation of a Lafayette polygraph and a Grass electroencephalograph, measurements of autonomic response were recorded for each individual under two conditions: (*a*) in a situation of relative relaxation, so as to provide resting-level records; and (*b*) in a standardized stress situation, so as to provide records of autonomic change. The stress condition devised for this study consisted of a simple arithmetic task to be completed under circumstances of distraction from a steadily increasing intensity of "white noise." A recording of music was provided during the relaxation to set up a control condition for the sensory stimulation involved in the stress task and to offer a uniform mental experience to all *S*s. The stimulation was given through an earphone attached to a Webster wire recorder. The music was selected from Bizet's *L'Arlésienne Suite*, a composition which is regarded as peaceful and relaxing. The arithmetic problem consisted of a series of one- and two-digit numbers, to be added by one *S* and to be subtracted from an initial large number by the next *S*, the answer being required at each step in the problem. In order to increase motivation and thereby to enhance the stress effects, each *S* was instructed, before the testing began, that his ability to solve the problem in spite of the distracting noise was a measure of his intelligence. Instruction was given also about the nature of the instruments, so as to minimize the occurrence of autonomic changes in response to the strangeness of the situation.

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[1] This paper is based on an investigation carried out in the department of psychology at The Catholic University of America, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The writer wishes to acknowledge the kindness of Dr. P. R. Hofstaetter, who directed the study.

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Under each experimental condition, relaxation and stress, continuous records of galvanic skin response and of relative blood pressure were obtained by means of the polygraph, while, simultaneously, records of electrical skin potential and of the heart cycle were obtained over two channels of the electroencephalograph. Time signals inserted on the records made it possible to coordinate the sets of data from the two instruments. Each recording was made over a period of 2 min., the first of which was taken up with the experimental task. In addition to the measurements obtained by these instruments, systolic and diastolic blood pressures were determined for the two conditions; and a single measure of dermographic latency was made.

Physiological Measurements

The various leads from the recording instruments were attached in the following manner. Electrodes moistened with standard electrolyte jelly were fastened to the palm and back of the left hand for recording changes in skin resistance; to the palm and back of the right hand, for recording changes in skin potential; and to the left ankle, to afford a lead II arrangement in conjunction with the electrode on the back of the right hand for the electrocardiogram. A standard blood pressure cuff was wrapped above the elbow of the left arm, and the bell of a stethoscope was fastened by elastic tape over the brachial artery at a point below the cuff.

Skin conductance. Log conductance level (log C-level) was calculated directly from the initial reading of resistance on the polygraph. Log conductance increment (log C-incr.) was calculated as the logarithm of the difference between the initial conductance level and the conductance level at the point of maximum increase. Records which indicated a decrease of conductance were scored simply as having zero increment; records which indicated a steady increase of conductance were measured at a point 45 sec. from the beginning of the stimulation, in lieu of a true maximum point; and records showing several maximum points of conductance were scored at the point of largest increase within a 45-sec. interval following the start of stimulation. Conductance recovery quotient (CRQ) was calculated as the difference between the maximum conductance increment under stress and the conductance increment at a point 30 sec. later, all divided by the maximum conductance increment under stress. It will be seen that the recovery quotients which appear in this study are based on the suggestions of Freeman and Katzoff (5).

Skin potential. Log potential activity level (log E-level) was calculated from the sum of the pen deflections in millimeters across a 30-sec. interval with mid-point corresponding in time with the point of maximum increase of conductance as determined in the manner just described. The sum in millimeters was multiplied by the calibration factor of the channel setting of the electroencephalograph to give the activity level in terms of microvolts. Log potential change (log E-change) was obtained as the logarithm of the difference between the activity level under stress and the level under relaxation. Potential recovery quotient (ERQ) was calculated as the difference between the activity level under stress and the activity level measured across a 30-sec. interval having its mid-point 30 sec. later than that of the stress interval, all divided by the activity level under stress.

Blood pressure. Resting-level systolic (SBP) and diastolic (DBP) blood pressures were obtained from the averages of auscultatory readings taken before and after the music stimulation. Changes in blood pressure due to stress (SBP- and DBP-change) were calculated as the difference between the resting-level pressures and the averages of the readings obtained immediately after the continuous recordings of stress activity. Relative blood pressure level (RBP-level) was obtained by means of a cuff attached to the polygraph and inflated to a point about 15 mm. Hg. above diastolic pressure. It was measured as the point of largest deflection of the pressure pen within a 30-sec. interval, having its mid-point at an instant of time corresponding with the point of maximum deflection of the PGR pen. The difference between the readings for the two experimental conditions was recorded as relative blood pressure change due to stress (RBP-change).

Heart period. The heart period (HP) was measured as the average of all the periods, from peak to peak of the QRS complex, across a 30-sec. interval with mid-point coinciding in time with the maximum conductance increment. The change in heart period due to stress (HP-change) was calculated as the difference between the period under stress and the period under relaxation. The heart period recovery quotient (HPRQ) was calculated as the difference between the heart period under stress and the heart period measured across an interval having its mid-point 30 sec. after that of the stress interval, all divided by the heart period under stress. The duration of the T-P interval (dur. T-P) was measured as the average length of time from the end of the T wave to the beginning of the P wave of the heart cycle. The change in the T-P interval owing to stress (T-P-change) was calculated as the difference between the measurements for the two experimental conditions. The heart period variability index (HP var.) was computed as the per cent increase of the average of three long heart periods over the average of six short periods during the relaxation condition. The long periods were selected at points about 10 sec. apart, with a short period lying on either side of a long one.

TABLE 1

Correlations between Autonomic Variables*

NO.†	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1																						
2	65																					
3	85	48																				
4	17	33	−07																			
5	54	41	90	17																		
6	34	52	57	07	22																	
7	35	34	22	33	−03	25																
8	10	−03	17	24	17	25	−26															
9	28	10	34	13	10	37	25	13														
10	22	02	−04	19	−01	−25	−07	−13	32													
11	−20	−18	07	−10	43	−77	−34	−22	−29	10												
12	03	17	04	00	10	−28	−07	−25	05	20	28											
13	00	00	00	22	−12	−22	−10	03	04	−17	20	−28										
14	−18	−13	−01	00	−02	−07	07	27	07	−05	−10	−07	10									
15	20	−01	−02	−07	−16	−27	54	−12	−29	−24	09	−32	−02	10								
16	−12	13	−13	−17	−10	−12	−10	21	10	−23	00	−22	−28	11	06							
17	07	−01	00	−17	22	−16	10	15	15	27	07	−09	−26	11	−20	58						
18	17	21	14	37	05	−25	−08	19	43	00	−15	−25	10	−30	02	02	−22					
19	−06	−13	−20	03	−18	−17	10	15	04	−29	−06	−22	−20	10	17	95	54	−04				
20	−26	−35	−22	−26	−18	−26	07	−07	12	00	−04	07	−33	07	−08	78	−22	−19	62			
21	26	−13	17	15	29	10	40	10	10	03	13	04	−20	11	12	42	30	−23	54	22		
22	03	−10	02	12	07	−12	−13	−13	13	−13	03	26	−10	34	10	02	−17	−13	02	−12	10	

* Decimal points omitted.

† The numbers refer to the following variables as described in the section on method:

1. log C-level
2. log C-incr. (music)
3. log C-incr. (stress)
4. CRQ
5. C + BP
6. C − BP
7. log E-level
8. log E-change
9. ERQ
10. SBP
11. SBP-change
12. DBP
13. DBP-change
14. RBP
15. RBP-change
16. HP
17. HP-change
18. HPRQ
19. dur. T-P
20. T-P-change
21. HP var.
22. Derm. lat.

Composite variables. Conductance plus blood pressure (C + BP) and conductance minus blood pressure (C − BP) were calculated in the manner suggested by Darling and Darrow (3). The sums and differences of normalized *T* scores for log conductance increment due to stress and change in systolic blood pressure due to stress were averaged for each individual.

Dermographic latency. This was measured in the manner recommended by Wenger and Ellington (16).

Temperament Measurements

The Guilford-Zimmerman Temperament Survey (6), which has reported reliabilities ranging from .75 to .87 and an internal validity based on item and factor analyses, was administered to each member of the group. In addition, a graphic self-rating scale of temperament was constructed and administered in an attempt to measure by self-ratings what Darling (2) and Wenger (14) measured by judges' ratings, as well as to measure self-rated aspects of the fourfold classification of melancholic, sanguine, choleric, and phlegmatic temperaments. It is admitted that both scales are concerned mainly with the *social* aspects of temperament.

As a measure of *psychomotor* aspects of temperament, each individual was requested to tap a telegraph key in circuit with an electrical counter. Tapping rates for 1-min. periods were obtained before and after the physiological measurements and were averaged.

Finally, as a measure of somatotype, which is of perennial interest in studies of temperament, the Rohrer index was computed.

RESULTS[3]

Of the 100 sets of records obtained in the manner just described, 85 were found to be without artifacts and were retained for the

[3] The reader is referred to the writer's doctoral dissertation, Variation in Autonomic Function as Related to Individual Differences in Temperament, May, 1953, on file in the Mullen Library, The Catholic University of America, Washington, D. C., for additional tabular and statistical materials.

study. Among the 22 autonomic variables in Table 1 are 11 measures of resting-level activity, 8 measures of change, and 3 measures of recovery. The intercorrelations in Table 1 were determined with the aid of the tetrachoric computing diagrams of Cheshire, Saffir, and Thurstone (1). The average standard error of the coefficients, as obtained by means of the tables published by Hayes (7), is .17. Since all the distributions had been dichotomized close to the medians, a general statement of significance, based on Hayes's tables, can be made: an r of .33 is significant at the .05 level, and an r of .44 is significant at least at the .01 level.

TABLE 2

Rotated Factor Loadings of the Autonomic Variables*

NO.	VARIABLES	FACTORS				h_j^2
		I	II	III	IV	
1	log C-level	86	14	−01	03	76
2	log C-incr. (music)	69	−02	17	−04	51
3	log C-incr. (stress)	83	17	−04	−12	73
4	CRQ	31	00	00	−18	13
5	C + BP	63	28	−44	−12	68
6	C − BP	55	−02	60	−14	68
7	log E-level	46	20	27	60	68
8	log E-change	11	34	17	−38	30
9	ERQ	30	28	04	−42	35
10	low SBP†	−15	02	35	14	16
11	decrease SBP†	10	03	71	−09	52
12	low DBP†	−04	05	55	−10	31
13	DBP-change	02	−27	04	−06	07
14	RBP	−10	19	−09	12	07
15	RBP-change	01	00	17	68	49
16	HP	−36	94	20	02	1.05
17	decr. HP	02	46	−16	04	24
18	HPRQ	17	00	17	−46	27
19	dur. T-P	−35	88	20	17	96
20	decr. T-P	−48	46	09	−03	45
21	HP var.	15	62	−16	26	50
22	Derm. lat.	02	09	−28	08	10

* Decimal points omitted.

† Variables have been reflected.

The table of intercorrelations was factored by the complete centroid method of Thurstone (13), and four factors were extracted. These were rotated by orthogonal rotation to simple structure and appear in Table 2.

Interpretation of Factors

In the development which follows, only those variables which have a factor loading equal to at least 2.58 times the average standard error of r will be considered as descriptive of the factor. This is proposed as a measure of the significance of the factor loading at the .01 level. Therefore, only those variables with loadings of .44 or greater will be included.

Factor I accounts for most of the variance (Table 3) in log conductance level and log conductance change measurements. It is of interest to see, as might have been anticipated, that log potential activity level belongs with this group of variables. Both conductance (Féré effect) and potential activity (Tarchanoff effect), no doubt, are related in some fashion either to presecretory or to secretory activity of the sweat glands. There is no clean-cut indication as to which branch of the autonomic nervous system may be predominant in this response pattern. It will be recalled that Darling and Darrow (3) proposed conductance plus blood pressure (variable 5) as an indicator of sympathetic activity, and conductance minus blood pressure (variable 6) as an indicator of parasympathetic activity. They fail as indicators here, since both of them have positive loadings on this factor. These composite variables will receive some discussion in relation both to their loadings on Factor I and to their loadings on Factor III. Variable 20, lengthening of the T-P interval, was included among the set of measurements of autonomic activity as a possible indicator of parasympathetic function. Lengthening of the T-P interval of the heart cycle is ascribed to increased vagal (parasympathetic) tone which blocks the impulse as it passes over the auricle from the sino-auricular node. With its negative loading on this factor, it is to be interpreted as "small decrease" in the T-P interval under

TABLE 3

Variables Contributing to Definition of Factor I

NO.	VARIABLE	LOADING
1	log conductance level	.86
3	log conductance change (stress)	.83
2	log conductance change (music)	.69
5	conductance plus blood pressure	.63
6	conductance minus blood pressure	.55
20	decrease in T-P interval (stress)	−.48
7	log potential activity level (music)	.46

conditions of stress. This interpretation is supported by the raw data for the variable: the direction of change for all but one individual was negative, the mean change being −.12 sec. Since variable 20 stands alone among six measures involving sweat gland activity, it can hardly specify the factor. The factor is presented, then, simply as a *conductance factor*, with the added implication that both branches of the autonomic system may be involved in it.

Factor II (Table 4) may be regarded as a response pattern involving a long heart period and a long T-P interval, with much variability in the length of the periods under conditions of relaxation, and a notable decrease in heart period and T-P interval under conditions of stress. Cursory inspection of the structure of this factor might lead one to suppose that the parasympathetic nervous system predominates here under resting conditions and the sympathetic nervous system predominates under stressful conditions. It is quite likely, however, that the notable decrease in the length of the heart period and T-P interval is simply a function of the initial length of the period under relaxation: the longer the period, the more of an opportunity there is for shortening. If this is the case, then the response pattern must be presented as a *heart period factor*, without attempt to designate which branch of the autonomic system predominates under either experimental condition.

TABLE 4

Variables Contributing to Definition of Factor II

NO.	VARIABLE	LOADING
16	heart period (music)	.94
19	duration of T-P interval (music)	.88
21	heart period variability (music)	.62
17	decrease in heart period (stress)	.46
20	decrease in T-P interval (stress)	.46

Factor III (Table 5) can be described as an autonomic response pattern involving a low diastolic blood pressure under relaxation and a fall in systolic blood pressure under stress. From this point of view, it would appear to be a factor of cholinergic activity or parasympathetic predominance. It is generally accepted that parasympathetic stimulation is associated with a drop in systolic blood pressure and with vasodilation in the aorta which may result in low diastolic pressure. For Factor I, it was seen that the two composite variables 5 and 6 could not be interpreted as diagnostic of the branch of the autonomic system which is responsible for the changes. Were it not for the peculiar structure of Factor I, on which these variables both have positive loadings, one would be inclined to regard the structure of Factor III as support for the rationale proposed by Darling and Darrow (3): conductance minus blood pressure, proposed as an indicator of parasympathetic activity, loads positively here along with two other variables which involve parasympathetic stimulation, while conductance plus blood pressure, proposed as an indicator of sympathetic activity, loads negatively. Since this interpretation is uncertain, however, the response pattern can be described only as a *blood pressure factor*.

TABLE 5

Variables Contributing to Definition of Factor III

NO.	VARIABLE	LOADING
11	decr. in systolic bl. pr. (stress)*	.71
6	conductance minus blood pressure	.60
12	low diastolic bl. pr. (music)*	.55
5	conductance plus blood pressure	−.44

* Variables have been reflected.

TABLE 6

Variables with Significant Loadings on Factor IV

NO.	VARIABLE	LOADING
15	relative blood pressure change (stress)	.68
7	log potential activity level (music)	.60
18	heart period recovery quotient	−.46

The combination of variables with significant loadings on Factor IV (Table 6) admits of no clear interpretation. Whatever this factor represents, it involves a large amount of sweat gland activity (Tarchanoff effect) under conditions of rest, considerable increase in relative blood pressure under stress, and slow recovery of normal heart period after disturbance. No attempt will be made to identify it more specifically.

Factor Scores

Since weighted standard scores in the factors of autonomic response were to be assigned to each individual in the group, loadings were selected from the rotated factors in Table 2 and multiplied by normalized T scores in the corresponding variables. The following equations were devised by linear combinations of the products: Factor I (conductance) = $.86(T_1) + .69(T_2) + .83(T_3) + .46(T_7) - .48(T_{20})$; Factor II (heart period) = $.94(T_{16}) + .46(T_{17}) + .88(T_{19}) + .46(T_{20}) + .62(T_{21})$; Factor III (blood pressure) = $.60(T_6) + .71(T_{11}) + .55(T_{12})$, where the numerical coefficient is the pertinent factor loading, T is the normalized standard score, the subscript refers to the variable, and the algebraic sign is that of the factor loading. Scores in the unidentified Factor IV are not included in this report. It will be noticed that the factor loadings in these equations are, according to the criteria mentioned previously, significant at the .01 level. Variables 5, conductance plus blood pressure, and 6, conductance minus blood pressure, were excluded from the equation for Factor I, since they could not reasonably be interpreted in the structure of that factor. In Factor III, however, variable 6 was retained to keep this factor somewhat comparable to Darling's (2) factor of "cholinergic activity," while variable 5 was eliminated because it appears that it is simply a negative way of expressing variable 6.

Response Patterns and Temperament

Normalized standard scores in traits of temperament were correlated with sets of weighted standard scores in the three factors of autonomic response. The tetrachoric computing diagrams of Cheshire, Saffir, and Thurstone (1) were used. Among 87 r's computed, only 4 are significant at about the .05 level. These are as follows: $-.34$ between Factor I (conductance) and the Guilford-Zimmerman trait *G* (general activity); .35 between Factor II (heart period) and the Guilford-Zimmerman trait *F* (friendliness); .38 between Factor III (blood pressure) and self-rated "sensitivity"; and .40 between the latter factor and self-rated "phlegmatic temperament." Since four correlations significant at the .05 level are what might be expected by chance alone in a table this large, no great certainty may be attached to them. They simply do not support the hypothesis under investigation in this study.

DISCUSSION

In view of the literature on the units of measurement of PGR, the significant and high correlations, .65 and .85, between log conductance level and the two measurements of log conductance change present some problems of interpretation. It is generally held that measurements of change should be independent of basal level, and Lacey and Siegel (11) present strong evidence to show that only conductance and log conductance satisfy this requirement. The present study does not bear this out. It is suggested that the high correlations may be dependent on some unknown bias in the recording system employed in this study.

As a by-product of this investigation, it had been expected that the high relationship between the Féré effect (conductance) and the Tarchanoff effect (potential activity), reported in the literature as summarized by McCleary (12), might be confirmed. Inspection of Table 1 reveals only a modest relationship at the .05 level of significance.

On the basis of Darling and Darrow's theorizing (3), it had been supposed that the two composite variables—5, conductance plus blood pressure, and 6, conductance minus blood pressure—might serve as reference variables for separating out the autonomic components of the factors. A study by Darling (2) has been tentatively interpreted as supporting these formulations. However, it should be remarked that Darling deviated considerably from the proposed rationale when he constructed the blood pressure portions of the equations from the sums of standard scores of systolic, pulse, and diastolic pressures, instead of employing simply the change in systolic pressure. The present study, in which the variables were constructed according to the original proposal (3), lends no experimental support to the formulations. In this instance, factor analysis has clearly succeeded in resolving these variables into their components: it has distributed the variance between Factor I (conductance) and Factor III (blood pressure).

Far from supporting the assumption of generalized autonomic balance and imbalance, the present investigation has separated out the various measures of autonomic response into factors representing mainly single organs and systems. The data are in close accord with the findings of Lacey and his associates (8, 9, 10) on autonomic response specificity, and offer rather strong support to the concept of specialized autonomic balance. Factor I is composed of measures involving mainly sweat gland activity; Factor II is composed entirely of heart period variables; and Factor III is composed of measures involving mainly blood pressure responses.

The relationships reported here between patterns of autonomic response and traits of temperament are so uncertain as to require little discussion. The correlations between autonomic activity and self-rated traits bear no similarity to the findings of Darling (2) and of Wenger (14). Nor can the correlations be compared with the results of a study in which Wenger (15) used the Guilford-Martin scales. The latter study, unfortunately, cannot be interpreted, because of the nature of the correlation matrix submitted to factor analysis. On the basis of the present study, then, one must conclude that there are no clearly demonstrable relationships between measures of traits of temperament and sets of scores in autonomic reactivity.

SUMMARY

The present study was designed to test the hypothesis that between sets of scores in autonomic function weighted with appropriate factor loadings and scores in traits of temperament there would be significant relationships. Measurements of autonomic response, involving both resting-level variables and change variables, were obtained from a group of 85 ostensibly normal, white, male college students under two conditions: (*a*) under relaxation while listening to music, and (*b*) under stress from an arithmetic task to be completed during distraction from noise. A 22-variable table of intercorrelations of autonomic functions was factored by the complete centroid method of factor analysis, and three factors described after orthogonal rotation: I, conductance; II, heart period; and III, blood pressure. The factorial structure offers strong support to the concept of specialized autonomic balance in place of the concept of generalized autonomic balance. Only four correlation coefficients significant at the .05 level were found between scores in factors and scores in traits of temperament as measured by self-rating scales and the Guilford-Zimmerman Temperament Survey.

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EFFECT OF BRAIN DAMAGE ON INTELLIGENCE IN RATS[1]

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A new type of test and a special developmental situation were used in this study to investigate two problems bearing upon the physiological basis of intelligence. According to the literature it seems (*a*) that any part of the rat cortex is as good as another in its contribution to problem solving, while in man this "equipotentiality" is not found if one compares the effects on the IQ of frontal lobe injury with parietal or temporal injury; and (*b*) that injury to the infant rat's cortex has much less effect on adult problem solving than adult injury, while in man, infant injury appears to have widespread and generalized effects on the IQ and adult brain injury often appears to have little or none.

Lashley found that the rat's capacity to form or retain maze habits was reduced in proportion to the amount of cortical tissue removed and was independent of the locus of the tissue. This relationship, the basis of the principle of mass action, was clearest on the more difficult types of mazes or latch-boxes (9, 10). The literature on human brain damage has, on the whole, failed to substantiate the principle (2, 6, 8, 12, 17). However, the type of test situation usually used in studying rat intelligence is a difficult learning task which has none of the diversity of the various subtests used in the human situation. Hebb and Williams (4) have suggested that rat intelligence could be assessed better with a "closed-field" test in which rats are presented with a variety of standard problems; in each test item the rat is required to solve quickly a simple problem and remember the solution for a few trials. A priori this test is more similar to the Binet type of test than a maze in which the rat may take some hundred trials to reach a criterion.

Tsang found very little effect on adult maze efficiency resulting from hemidecortication of infant rats (15), whereas brain-damaged children show a declining IQ (14) and a generalized intellectual impairment (2). The type of cage in which laboratory rats are usually reared has none of the diversity of the situations in which human intelligence develops. When normal rats are reared as pets, or reared in a large, complex box in a laboratory, they perform better in the closed-field test at maturity (3, 5). Unimpaired cerebral efficiency may be of considerable importance for such "free-environment" rats in developing their adult intelligence.

The present study, therefore, re-examined the effects of brain damage on rat intelligence, and the difference between infant and adult injury, with the new closed-field test and with rats reared in a complex environment considered to be more nearly analogous to the human situation.

METHOD

Subjects

Of an original population of 116 male hooded rats, 28 died as a result of operations. The results from 18 cases were discarded on the basis of necropsy study showing operative damage to subcortical structures, or lesions too extensive in other respects (e.g., some large anterior lesions extended into the posterior half of the brain and so could not be treated as "anterior"). This study is based on the records of 70 animals: 13 normals and 57 operates.

Procedure

The general plan of the experiment was to operate upon three different areas of cortex, in one group of rats at infancy and another group at maturity. During growth and the recovery period for the adult operates, the animals were exposed to an environment which contributes to the development of rat "intelligence."

Rearing. All rats were handled frequently throughout their growth. From the twenty-third day of age until the one-hundred and nineteenth day the rats were exposed to a complex environment. This exposure was about 2 hr. per day for the first week, thereafter almost 12 hr. per day except for approximately ten days at the time of operating on the adult rats. During this period all rats were kept in their cages. Total exposure time to the complex environment was approximately

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[1] This study was conducted under the direction of Prof. D. O. Hebb in partial fulfillment of the requirements for the doctoral degree at McGill University. The research was supported in part by grants from the Defence Research Board.

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660 hr. Seven staggered groups with different dates of birth were used so as not to crowd the rearing and testing program.

The complex environment consisted of two wooden boxes, each 42 by 48 in. and 8 in. high, connected by a passageway. The top of the boxes was made of ½-in. wire mesh. The boxes contained food and water, and a variety of wire and wooden structures: low alleyways, mazelike sections, enclosures, etc.

Testing. When they were 119 days old, the rats were placed in colony cages and fed only twice a day in the testing program. The test method was that described by Rabinovitch and Rosvold (13) except that 24 test items rather than the new 12 were used. In this test, the rat is first accustomed to being handled and oriented with respect to a starting box and goal box in an enclosed field. After preliminary training, the test problems, in which the rat must by-pass simple barriers to get to the food, are presented. Preliminary training is completed when the rat reaches the criterion of nine runs in 60 sec. of running time, measured from the time of placing the rat in the starting box to the time of taking a bite at the food. All the rats met the criterion in five days.

Two problems were given each day, one in the morning, the other in the evening. Errors were recorded whenever a rat deviated from the direct path into designated zones of the field. The rats were given ten runs on each test problem.

Surgical and histological. Operations were performed under deep ether anesthesia with antiseptic technique. The cortical tissue was removed by suction through fine glass tubing. Infant lesions were made at 18 to 20 days of age and adult lesions at 74 to 76 days. The loci of the lesions are classified as bilateral posterior, bilateral anterior, and unilateral.

After testing, the operated animals were brought to necropsy. The brains were removed, fixed, sectioned (at 40 micra), and stained with thionin. At least every eighth section was mounted for the bilateral lesions; for most unilateral lesions, every tenth.

Reconstructions of the cortical lesions were made on the conventional Lashley rat brain diagrams. However, the usual procedure was modified in an attempt to cope with the tendency of brain tissue, after early operations especially, to shift into the area of operation and so cause an underestimation of the extent of damage.

A set of cross-sectional diagrams corresponding to Lashley's levels 2 to 17 were drawn and reverse blueprint copies obtained. The linear extents of pyriform cortex and of neocortex in normal sections appeared to have a reasonably constant relationship for any given level. Therefore, the appropriate magnification for the projection microscope was judged mainly by matching the extent of pyriform cortex of a particular section with that of the standard diagram. The diagram was then marked to indicate the amount of cortical tissue remaining on each side of the lesion. Thus, the picture of the lesion was enlarged by an amount equal to any decrement caused by filling in the gap through shifting of brain tissue. Appropriate marking of the diagrams was easiest in the unilateral lesion group, where the normal side offered a check of the normal amount of neocortex.

The extent of damage indicated on the cross-sectional diagrams was transferred with proportional dividers to the Lashley diagrams. The area of the lesions was measured with a planimeter and expressed in terms of percentage of the total area of the neocortex.

The amount of degeneration in the lateral geniculate nuclei in both the unilateral and bilateral-posterior lesion groups was also determined. The condition of these nuclei is a more reliable measure of the extent of visual field defect than locus of cortical destruction, and visual factors appear to have considerable importance for performance in the closed-field test. Diagrams of a maximal cross section of the nucleus were prepared according to Lashley (11), and the locus and amount of degeneration were marked upon them.

The extent of degeneration was easier to determine in the unilateral lesion group, as the opposite side offered a normal nucleus for immediate comparison. Accordingly, the partly degenerated nuclei of the whole unilateral lesion group were arranged in order of amount of cell loss. These 20 cases were then used as a 20-point scale for assessing destruction of the nuclei of the bilateral lesion cases. The scale covered almost the whole range of possible degeneration of the dorsal part of the nucleus.

RESULTS

The results for the operated rats are considered under four main types of lesion: anterior, unilateral, early posterior, and late posterior.

Anterior lesions did not extend back beyond Lashley's level 9, and posterior lesions did not extend forward beyond level 8½. The unilateral lesions ranged over almost the full length of the brain. All the posterior and unilateral lesions, and none of the anterior lesions, involved the striate area. Table 1 shows the means and standard deviations of the amount of cortical destruction in terms of percentage of the total area of the neocortex, for each group of animals.[3] Unilateral lesions as a group were much larger than the bilateral-posterior lesions, and bilateral-posterior larger than bilateral-anterior lesions. In each of these groups, also, early lesions tended to be larger than late lesions.

The means and standard deviations for the

[3] To save printing costs, four pages of standard rat brain diagrams showing locus of lesion, percentage of neocortex destroyed, and number of errors for each operated animal have been deposited with the American Documentation Institute. Order Document No. 4110 from ADI Auxiliary Publications Project, Photoduplication Service, Library of Congress, Washington 25, D. C., remitting $1.25 for 35 mm. microfilm or $1.25 for 6 by 8 in. photocopies. Make checks payable to Chief, Photoduplication Service, Library of Congress.

error scores are tabulated for the various groups in Table 1. The mean test score of the anterior lesion group does not differ significantly from the normal test score. The test scores of the unilateral lesion group are significantly worse than normal. Scores for the rats with early unilateral lesions are not significantly different from those with late lesions. The group with the posterior lesions showed the greatest effect of operation. Within this group the animals with lesions made in infancy had the better test scores.

The first point of interest in these results is the lack of effect of anterior lesions on test scores. These lesions were smaller than the unilateral or posterior lesions, but their size does not account for the lack of effect. By excluding the six largest lesions in the posterior group, a group of 12 posterior lesions is obtained with a mean size of 12.3 per cent cortical destruction, compared with 12.5 per cent for the total anterior group of 19 animals. But the mean error score for the 12 animals with posterior lesions is 335, compared with 185 for the anterior group. This large difference occurred despite the fact that the volume of cortex destroyed is greater for the anterior group in the comparison: the determination of size of lesion is in terms of area, and much of the frontal cortex is thicker than cortex at the striate area. Excluding the late-posterior group from consideration because of heterogeneity of variance in their test scores, analysis of covariance confirmed that the difference in performance between anterior and early-posterior lesion groups was not a result of the difference in lesion size (*F* ratio, 24.0; *p* less than .001).

TABLE 1

Relation between Size of Lesion and Error Score for Various Groups

GROUP	*N*	% CORTEX DESTROYED		ERROR SCORE		CORRELATION (*r*) OF ERRORS WITH LESION SIZE
		Mean	*SD*	Mean	*SD*	
Anterior early	9	15.3	4.8	194.2	44.6	−.19
Anterior late	10	9.0	4.4	176.5	27.4	.06
Total anterior	19	12.5	5.3	184.9	37.6	.05
Posterior early	11	19.6	8.6	342.0	66.8	.49
Posterior late	7	15.0	10.9	410.0	169.2	.83
Total posterior	18	17.8	9.8	368.4	122.3	.58
Unilateral early	12	35.8	7.9	285.4	53.1	.33
Unilateral late	8	26.4	11.0	287.1	64.3	.77
Total unilateral	20	32.1	10.3	286.4	57.9	.50
Normal controls	13			194.0	42.6	

Table 2 shows the means and standard deviations of the amount of degeneration in the lateral geniculate nuclei. Analysis of covariance indicated that the effect of damaging the striate cortex, in terms of the geniculate degeneration, was similar in both the posterior and unilateral groups. Less efficient performance appeared to depend on the extent to which a lesion encroached upon the posterior cortex, regardless of whether the damage was unilateral or bilateral.

TABLE 2

Relation between Degeneration in Lateral Geniculate and Error Score

GROUP	*N*	DEGENERATION RATING		CORRELATION (*r*) OF ERRORS WITH DEGENERATION RATINGS
		Mean	*SD*	
Unilateral early	12	11.4	5.3	.29
Unilateral late	8	9.1	6.1	.62
Total unilateral	20	10.5	5.8	.44
Posterior early	11	28.0	9.3	.70
Posterior late	7	18.1	9.4	.87
Total posterior	18	24.2	10.5	.50

The data do not allow an analysis of the effect of damage to the posterior brain apart from striate damage, since lesion size and lateral-geniculate degeneration correlated in the present study. The rho's for the unilateral and posterior lesion groups were .75 and .66, respectively.

DISCUSSION

By using a new type of rat "intelligence test" and rearing the rats in a complex environment, results have been obtained which are different from those obtained in previous rat studies of cortical function, and which are more similar to the human brain-damage data.

The lack of deterioration of test scores in the anterior lesion group was shown to be the result of the locus and not the size of the lesion. The test was designed, after the fashion of

Emotional Conditioning and Extinction

The conditioned emotional response (CER) was established in Skinner boxes in accordance with our standard procedure (10, 11). In brief, all animals first were trained in lever pressing until they showed a stable output of lever responses for an aperiodic water reward. Then, during Skinner-box runs, all animals received two emotional conditioning trials, each consisting of a 3-min. presentation of the CS (a clicking noise) terminated contiguously with two momentary electric shocks to the feet as the UCS (approximately 1.5 ma.), delivered through the grill floor of the apparatus. These conditioning trials were spaced a day apart, with an adaptation run in the Skinner box, without presentation of CS or UCS, on the intervening day to minimize generalized fear reactions to the apparatus.

Those animals not showing at least an 80 per cent reduction in lever-pressing output during the 3-min. CS (as compared with the output during the 3 min. preceding the introduction of the CS) on the second conditioning trial received a third CER conditioning trial on the following day. This method was employed to avoid conditioning too strong a CER in those animals which acquired the response rapidly. The results for the two- and three-trial animals will be combined in the present discussion because careful analysis revealed no material or significant differences in either their subsequent performance or response to the experimental treatment.

The animals had daily 12-min. runs in the apparatus. A record was kept of the total number of lever responses made by the end of the third, sixth, ninth, and twelfth minute of each run by each animal. On conditioning days, the CS was introduced at the end of the third minute and terminated with presentation of the UCS at the end of the sixth. Here the CER appears as a reduction or cessation in lever pressing during presentation of the CS. The *inflection ratio* (see 11) describes the magnitude of the CER. Briefly, this ratio expresses the difference in output between the second and first 3-min. segments of the curve—the effect of presentation of the CS upon rate of lever pressing—as a proportion of the output during the first 3-min. segment. If the CS produces no change in output, the ratio is 0.00; if the animal has a strong CER and makes no lever responses during the CS, the ratio is -1.00; if a strong CER with a ratio of -1.00 or $-.90$ is attenuated, the ratio shifts in the positive direction toward 0.00; and so on.

After conditioning and five days after the last experimental treatment, all survivors were tested for retention of the CER by an unreinforced presentation of the CS during a Skinner-box run. Then, on each of the next nine days, the animals received an unreinforced presentation of the CS to extinguish the CER.

All animals were on a 23-hr. water-deprivation schedule during conditioning and extinction, with free access to food in the home cages. All had free access to water as well during the treatment period.

Experimental Treatment with CS_2 and Ether

After the last emotional conditioning trial, the animals were divided into groups matched for magnitude of the CER on the last conditioning trial and with an equal distribution of two-trial animals to all groups.

Group I received 13 CS_2 inhalations, each to the point where a generalized convulsion occurred, 1 on the first day and 2 on each of the next 6 days. About 2 hr. after each convulsion, these animals were given ether anesthesia to the point where the corneal reflex disappeared. Treatment started on the fourth day after the last conditioning trial (N = **11**, 6 survived).

Group II received 13 CS_2 convulsions as above, but no ether anesthesia (N = **11**, 8 survived).

Group III received 13 CS_2 inhalations as above while under ether anesthesia so that convulsions did not occur (N = 11, 8 survived).

Group IV served as an untreated control group which received equivalent handling only (placed in inhalation jars, etc.) (N = 23, all survived).

Group V received 14 ether inhalations to the point of anesthesia (loss of corneal reflex), but no CS_2, following the schedule employed in the treatment of the animals in group II (N = 11, all survived).

The CS_2 treatments, when given more than once per day, were separated by intervals of 6 to 8 hr. CS_2 was administered as follows: About 5 min. prior to each session, a cotton pad well soaked with CS_2 was placed in a covered desiccating jar to permit adequate diffusion of vapor throughout the jar. Then each animal receiving an inhalation was placed in the jar individually to remain there with the soaked pad either for 3½ min. or for 30 sec. after the beginning of the generalized clonic convulsion, whichever came first. If respiration failed during the inhalation period, the animal was removed, given artificial respiration by nose tube, and then returned to the jar to remain there until he received the standard exposure to CS_2 vapor. In most cases, the unanesthetized animals exposed to CS_2 developed convulsions well before the 3½-min. time limit. All but four showed at least a light generalized convulsion during each treatment; these four died on the day they failed to show a convulsion, and they did not contribute to the results.

The procedure for ether anesthesia was identical with that described in an earlier paper (12). Briefly, a cotton pad well soaked with ether was placed in a desiccating jar and the vapor allowed to diffuse. Then each animal to be anesthetized was placed individually in the covered jar until it lost the corneal reflex. The anesthetized animals receiving no further treatment were removed immediately to the home cage. Those animals receiving ether prior to CS_2 to block the convulsions (group III) were removed immediately to the CS_2 jar, where they remained for 3½ min. No group III animal ever showed any convulsive activity.

A fresh supply of Carbon Disulphide Merck (reagent) and Ether Squibb (for anesthesia) was opened for each treatment session. All treatments were conducted in the brisk draft of a large exhaust fan as a precaution against toxic effects upon the *E*s.

The ether anesthesia was included as a procedure for some groups to allow us to determine whether the convulsions, CS_2 vapor, anesthesia, or some combination of these produced the attenuation in the CER. Groups I and III had equal exposure both to CS_2 and ether, but only group I had convulsions. Similarly, groups II and V were confined and given an inhalation procedure (either CS_2 or ether) which might have been mildly irritating or disturbing, but only group II had convulsions. Group IV, of course, provided the control for the effects of handling and confinement in the desiccating jars upon the CER.

Group IV is disproportionately large because the experiment was performed in two stages, each having its own set of untreated animals to control for any influence fluctuations in temperature and humidity might have on the CER. The data for the two sets of control animals did not differ materially or significantly, so they are combined to permit each experimental group to be compared with a common control group. Group V, which received ether only, was in the first stage of the experiment and received 14 treatments. The other experimental groups were in the second stage and received only 13. The unexpectedly high mortality made it advisable to terminate the treatments at this point, contrary to the original plans, in order to save enough animals for the retention tests. Because nothing in the results indicated that the extra ether treatment given the animals in group V influenced their performance or their comparability with the other experimental groups in any significant way, no new ether-only group, with 13 rather than 14 treatments, was run.

RESULTS

The CS_2 inhalations successfully produced convulsions, just as reported by Griffiths and Wolfe (7). The CS_2 vapor in the desiccating jar did not appear to be more irritating than ether vapor, though it did seem to disturb the animals more than air alone. The animals typically moved about and actively explored the jar, perhaps for avenues of escape, but showed no signs of violent activity or intense pain.

Each convulsion tended to follow a characteristic course, with considerable variation in the latency and duration of each phase. After 1 to 3 min. of inhalation, the animals showed shallow breathing and some ataxia. Next, following a few scattered clonic twitches of the extremities, many animals developed opisthotonus, which merged into a brief quasi-tonic general immobility. A generalized clonic convulsion then emerged from the tonic immobility or developed directly out of the scattered clonic twitches, persisting in varying degrees for several minutes after the animal came out of the jar. Typically, treated animals appeared somewhat ataxic and "confused" for 5 to 10 min. after the generalized clonic convulsion.

In general, the convulsions appeared to be considerably less severe than those produced by electroconvulsive shock. The tonic phase always was brief, often hardly noticeable, while the clonic contractions usually resembled those produced by insulin hypoglycemia. Respiratory failure produced a substantial portion of the deaths. With one exception, the other casualties were found dead in their cages some time after what had appeared to be entirely satisfactory convulsions. The exception died when a uniquely severe clonic contraction thrust his head against the heavy cover of the desiccating jar and presumably fractured his skull, as indicated by the sudden and profuse rhinorrhea he showed immediately afterwards. As with electroconvulsive shock, though not necessarily for the same reason, animals subjected to the convulsions typically tended to become somewhat irritable. Animals surviving the CS_2 treatments, either convulsions or inhalations only, appeared healthy and well groomed at the time of the posttreatment tests.

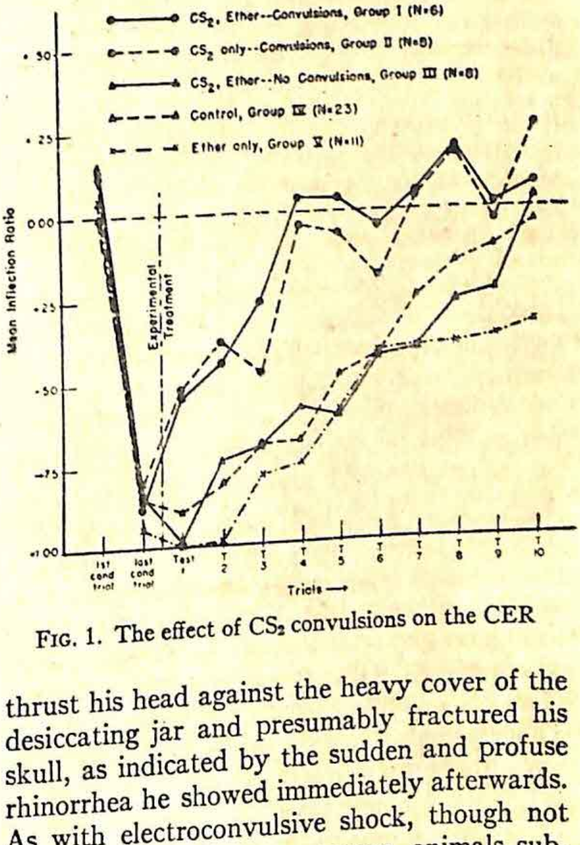

FIG. 1. The effect of CS_2 convulsions on the CER

Figure 1 presents the main findings in terms of the mean inflection ratio for each group for the first and last emotional conditioning trials and the retention tests (extinction trials) T_1, T_2, and so on. The sharp negative shift in the ratios between the first and last conditioning trials reflects the development of the CER as a function of conditioning. The positive shift in the mean ratios for groups I and II from the last conditioning trial to T_1 reflects directly the attenuation in the CER produced by the CS_2 convulsions. In contrast, those groups which had some form of treatment but no convulsions (groups III and V) showed essentially unchanged or slightly stronger CER's on T_1, as indicated by the small negative shifts in the mean ratios over the same period. The difference between groups I and II combined and the control group (IV) in the number of individual animals showing such positive shifts is significant ($\chi^2 = 5.01$, $p < .05$),[2] whereas this difference between groups III and V combined and the control group is not ($\chi^2 < 1.00$, $p > .10$). Animals that had CS_2 convulsions showed evidence of attenuation in the CER after treatment, though the attenuation was less dramatic and clear-cut than ECS usually produces.

Groups I and II combined similarly showed more rapid extinction of the CER than did the control group; groups III and V combined did not differ from the controls in this regard. The mean inflection ratios for groups I and II returned to the normal preconditioning level by the fourth extinction trial; the remaining groups' ratios returned to this level much later if at all during the ten extinction trials. To provide distributions for statistical tests, each animal's average inflection ratio for trials T_1 through T_4 was taken to indicate the rate at which the CER decreased in strength in that animal as a function of experimental extinction. The average of these means for each group gave the rate of extinction for that group. With performance scored in this way, groups I and II combined showed significantly more rapid extinction than the control group ($v = 3.57$, $p < .01$), whereas groups III and V combined did not ($v < 1.00$, $p > .10$). The statistic v was employed, in preference to t, to reduce the biasing effect of unequal N's and the somewhat heterogeneous variances (8, 16).

Group III, which had CS_2 under ether anesthesia to block the convulsions, showed no attenuation in the CER after treatment. The differences between group III and the untreated control group (IV) in rate of extinction of the CER and in changes in amplitude of the response from the last conditioning trial to T_1 were small and not significant. In fact, groups III, IV, and V (which received ether only) showed no material or significant differences in the strength of the CER after treatment. Nor did ether anesthesia, added to the effects of the CS_2 convulsions in group I, produce any greater attenuation in the CER than CS_2 convulsions alone produced; groups I and II showed only small and nonsignificant differences after treatment. These negative findings on the effects of CS_2 vapor and ether anesthesia are interesting because of the inhibitory influence both substances are supposed to have upon cerebral metabolism (4, 9, 15, 18). It is not impossible, however, that either or both might turn out to have a very small effect on the CER, if a more sensitive test could be devised.

The data clearly indicate, however, that the convulsions themselves have far the more important effect. This comes out very clearly again in the comparisons between groups I and III, both of which had CS_2 and ether. Group I, which had convulsions, showed significantly greater reduction in the amplitude of the CER from the last conditioning trial to T_1 ($v = 2.20$, $p < .05$) and significantly more rapid extinction ($v = 2.30$, $p < .05$). As with ECS, the convulsion rather than the convulsant stimulus plays the critical role in the attenuation of the CER.

CONCLUSIONS

1. CS_2 convulsions attenuated the CER, as measured either by decreased amplitude of the response or decreased resistance to extinction after treatment. This effect of CS_2 convulsions, though similar in direction to that produced by ECS, was much less marked and dramatic.

2. As with ECS, the attenuation did not appear if intercurrent ether anesthesia prevented the convulsions. Animals receiving both CS_2 convulsions and ether anesthesia, at different times during the day, showed significant attenuation, however. The convulsions, rather than the convulsive stimulus as such, appear to be critical in reducing the strength of the CER.

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[2] Chi-square values are corrected for discontinuity.

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PICTURE PERCEPTION IN A HOME-RAISED CHIMPANZEE[1]

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Since the chimpanzee's acquisition of cultural intelligence is seriously hampered by its limited ability to understand human language (2, p. 201), we have been interested in the extent to which other, nonlanguage modes of communication may serve partially to offset this deficiency. We have shown that imitation can provide one such alternative channel (3). The present investigation is concerned with the chimpanzee's understanding of pictorial representations—another communications medium of considerable importance in human culture.

We have found only two references to the chimpanzee's picture perception in the literature. Köhler (5, p. 337) reports that his *S*s showed interest in photographs of chimpanzees, and that two of them, trained to choose a picture of bananas in a discrimination experiment, transferred readily to a new and different picture of bananas. The Kelloggs (4, p. 296) report that at the age of 15 months Gua could point out drawings of a dog and a shoe, on command. Pictorial stimuli were used extensively in the studies of monkey intelligence at the University of Liége; they have been reviewed quite critically by Lashley (6).

The *S* in the present investigation is Viki, a chimpanzee whose first five years have been spent in the authors' home. Her background of experience is much like that of a human child, with the usual opportunities to see a great variety of pictures. A detailed description of her first three years has been published elsewhere (2). We have never attempted to *train* her in picture perception; the experiments reported here were intended simply to *test* whatever ability she might have acquired spontaneously. It is possible, however, that her performance may have improved slightly during the course of the investigation, owing to experience incidental to testing.

OBSERVATIONAL DATA

At about 18 months, Viki began to spend an increasing amount of time looking at books, magazines, catalogs, and newspapers, and this has continued to be a common play activity until the present time. At first, she turned the pages and looked at the pictures but seldom responded differentially to them. Distinctive reactions soon began to appear, however, as illustrated by the following examples.

When she was 26 months old, she found a page of colored pictures of bizarrely costumed dolls, which she slapped vigorously whenever she encountered it. She did not react this way to the colored pictures of people on other pages.

At three years, she leaned down and put her ear to a picture of a wrist watch in a magazine (2, p. 201). She repeated this several times when told to "listen." (She had presumably not mistaken it for a real watch, since her normal reaction would then have been to attempt to pick it up and hold it to her ear. Her apparent supposition that the picture might tick is not surprising in view of her age and her experience with sound movies.)

On several occasions, since the age of four years, she has pointed to pictures in beverage advertisements, said "cup," and led one of the *E*s to the kitchen for a drink. She once tapped a picture of a candy bar in an advertisement, made "food barks," and led *E* to the household supply of the same kind of candy.

At four and one-half years, she took the magazine she was looking at to one of the *E*s, tapped a picture of a highball, and said "cup," but then refused a drink. (This is one of the few instances we have observed in Viki of apparent communication for its own sake, rather than with a practical purpose.)

PRELIMINARY EXPERIMENTS

Between two and one-half and three and one-half years, Viki's picture perception was tested sporadically by means of the matching technique, with which she was already familiar

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[1] This investigation was assisted by grants from the Penrose Fund of The American Philosophical Society and from the Samuel S. Fels Fund.

(2, p. 126). She was required to choose that one of two familiar objects which was shown in a picture held up as a model. Her performance was quite variable, but she chose correctly on 78 per cent of 92 trials. Since the object shown in the picture was often identical to one of the choice objects, matching on the basis of color or form might have accounted for her success.

At three and one-half years, we tested her ability to imitate actions illustrated in pictures. We prepared black and white pictures showing various items of the "imitation set series" (3, p. 452) being performed by several different people, and by Viki herself. (Sample items are clapping hands, patting head, and protruding tongue.) We used motion pictures first, then projected stills, then photographic prints, and finally simple line drawings. She performed fairly well from the first session on, and transferred readily through the various stages from movies to line drawings. She accepted the procedure as a game at first, and would often work without being rewarded for correct responses. (She occasionally "ran herself on the experiment" by plugging in the movie projector and turning it on, or by getting the pictures and spreading them out on the floor.) This procedure was ill adapted to quantitative analysis: we could not define chance performance, since the chance probability of her doing a given item depended on her preference for it and on its familiarity—both of these factors being quite variable. She seldom failed to imitate preferred actions (those which she often performs spontaneously, in play), but she often made errors by performing such preferred actions in response to pictures of nonpreferred items. This type of error sometimes occurs when the demonstration is given by a real person and does not necessarily indicate poor picture perception.

GENERALIZED DISCRIMINATION EXPERIMENT

We investigated Viki's picture perception more extensively when she was about five years old, using a modified discrimination procedure. She had recently served as an *S* in a study of discrimination learning set (1) and had achieved a high level of second-trial accuracy (96 per cent) in object discrimination problems.

Method

The *generalized discrimination* procedure differed from customary discrimination procedure in that a new pair of pictures was used for each trial. The same two classes of objects (e.g., chairs and automobiles) were illustrated in all trials of a given problem, but each trial involved new pictures of different members of these classes. A problem involving 12 pictures of automobiles, for instance, would include a mixture of sizes, body styles, and angles (as well as colors, when colored pictures were being used). These pictures could then be consistently discriminated from 12 similarly varied pictures of chairs only by recognition of the class of objects illustrated. (We found it necessary to avoid certain classes of objects because the pictures available tended to be too uniform in color and form; refrigerators, for instance, are almost invariably white and rectangular.)

This procedure may be thought of as requiring the *S* to utilize conceptual ability in addition to picture perception. For the present purpose, we attempted to minimize the conceptual demands by making the concepts narrow (e.g., "dog," rather than "animal"), and by requiring discrimination between markedly different concepts (e.g., "dog" vs. "flower," rather than "dog" vs. "cat").

The pictures used always illustrated things which were familiar to Viki. Some of them were cut from magazines, newspapers, and catalogs, some were photographic prints, and some were specially prepared line drawings. The pictures were mounted on white cards—usually 5 by 8 in. in size, occasionally smaller. The toss of a coin determined which class of pictures would be correct in each problem.

On each trial one of the two food wells in a wooden tray was baited with a food reward, and each well was covered with a picture. This was done behind an opaque screen. The screen was then removed, and Viki was allowed to displace one of the pictures. In case of an error, she was required to wait a few seconds before correcting. When she chose correctly, and had taken the reward, she was permitted to displace the remaining picture, if she wished, but she very seldom did so.

The number of trials per problem varied, but averaged about 12. One problem was presented at each daily session. There were 28 problems, in four successive groups. Group A consisted of 7 problems in which all pictures were realistic and in natural color. Group B consisted of 6 problems utilizing an assortment of pictures ranging from color photographs to highly stylized black and white drawings. Group C was intended to evaluate the importance of color. It consisted of 7 problems, each of which contained approximately equal numbers of pairs of colored pictures and black and white pictures, all realistic in form and shading. Group D consisted of 8 problems in which all pictures were line drawings made with black ink on white paper. Many of them were freehand copies of realistic pictures used in earlier groups. Some of these drawings are shown in Figure 1.

Table 1 lists the classes of objects illustrated by the pictures in each individual problem.

Results

Since the first trial of each problem served only for training, and gave no indication of ability, results are presented in terms of the remaining trials. Table 1 shows the percentage of correct responses in each group of problems. Each of these percentages is significantly different from 50 per cent at better than the .0001 level of confidence. Scores for individual problems are not given, since each one would be based on too few trials to be reliable.

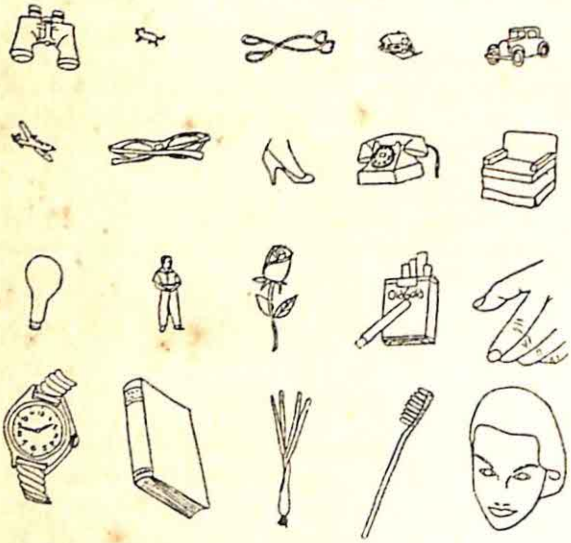

FIG. 1. Some of the line drawings used in the generalized discrimination and matching experiments

There was no appreciable tendency for performance to improve from problem to problem within any group, nor from trial to trial within problems (beyond the first trial).

In group C, there were 37 trials utilizing black and white pictures, of which 68 per cent were correct, and 39 trials utilizing colored pictures, of which 95 per cent were correct. The difference between these percentages is significant at the .005 level of confidence.

GENERALIZED MATCHING EXPERIMENT

Method

Immediately after completion of the generalized discrimination work, our *S* was tested on generalized matching. The sample, or model, was a real object, and a choice was required between two pictures, one of which illustrated an object of the same class as the sample. Successful matching on the basis of size was impossible, since picture size was unrelated to object size. Color matching was ruled out in the case of colored pictures, either by using two pictures of the same pre-

TABLE 1

The Four Groups of Generalized Discrimination Problems

GROUP A (REALISTIC COLORED PICTURES)			GROUP C (REALISTIC PICTURES)		
	+	−		+	−
1	drinking vessel	woman's face	1	watch	chair
2	automobile	shoe	2	spectacles	cigarette lighter
3	cigarette lighter	bird	3	automobile	dog
4	man	food can	4	child	food
5	child	flower	5	drinking vessel	man
6	hand	face	6	food can	flower
7	food	automobile	7	shoe	woman
79 trials, 85% correct			76 trials, 82% correct		
GROUP B (ASSORTED TYPES OF PICTURES)			GROUP D (BLACK AND WHITE LINE DRAWINGS)		
	+	−		+	−
1	dog	chair	1	dog	automobile
2	cat	house	2	shoe	chair
3	woman	automobile	3	drinking vessel	child
4	telephone	watch	4	face	hand
5	face	shoe	5	cat	house
6	airplane	dog	6	telephone	airplane
			7	dog	shoe
			8	automobile	chair
61 trials, 75% correct			101 trials, 73% correct		

dominant color, or by using a sample object which differed in color from its illustration. Form matching would have been very difficult, at best, because of the changing orientation of the sample object. The incorrect picture always showed an object which could have been used as a sample; never, for instance, a house or a tree. Toy objects were sometimes used as samples for pictures of real dogs or automobiles.

There were no "problems," in the sense of a series of related trials. Each trial was independent, with a new sample object and a new pair of pictures illustrating a new pair of classes of objects. There were 97 trials, in four successive groups, with 10 to 14 trials per session.

Group E consisted of 37 trials using realistic color pictures, most of which had previously been used in the discrimination experiment in different combinations. (To insure that *S* actually looked at the sample before making a choice, we handed the sample object to her and let her examine it for a few seconds. Unfortunately, she sometimes ran off to play with it, temporarily abandoning the experiment, so this procedure was not used in later groups.)

In group F, 13 picture pairs from group E were reused with reversed polarity and new samples. In this group, the *S*'s attention was attracted to the sample, which was then concealed, and a period of 10 sec. was allowed to elapse before the screen was raised and *S* was allowed to displace a picture.

Group G consisted of 25 pairs of line drawings of the type shown in Figure 1. (A few of the drawings originally used in group D of the discrimination experiment were included, in new combinations.) In this and the following group, the sample object remained in sight during the response.

Group H consisted of 22 pairs of line drawings from group G, arranged in new pairs, each consisting of two previously correct or two previously incorrect pictures.

Results

Percentages of correct responses for each group were: group E, 95 per cent correct; group F, 85 per cent correct; group G, 80 per cent correct; group H, 91 per cent correct. These values each differ from chance at better than the .005 level of significance.

DISCRIMINATION OF PICTURES AND NONSENSE DESIGNS

Discrimination problems are ordinarily learned more quickly when the stimuli are three-dimensional objects than when they are designs on flat surfaces. One might predict, therefore, that picture discrimination would be easy, since the stimuli represent three-dimensional objects; or that it would be difficult because the stimuli are, physically, designs on surfaces. To clarify this point, we compared Viki's performance on discrimination of pictures and nonsense designs.

Method

The *S* was trained to a criterion of five successive correct choices on each of 25 discrimination problems, using a single pair of stimuli throughout each problem. In problems 1, 3, 5, . . . 25, the stimuli were realistic, colored pictures. In problems 2, 4, 6, . . . 24, the stimuli were simple nonsense designs, drawn with crayons on white cards. In either case, the two stimuli in a given problem differed in form, size, and color. The pictures also differed in the familiar objects which they represented; but the nonsense designs did not clearly represent any objects. The pictures, being realistic, each contained several colors, but each design was drawn with a single color.

Results

Performance may conveniently be scored in terms of mean errors per problem, not counting first-trial errors. These values (with standard errors) are: .8 ± .3 for pictures, and 2.7 ± .5 for nonsense designs. The difference is significant at the .002 level of confidence.

DISCUSSION

It would have been surprising, in a sense, if Viki had proved completely lacking in picture comprehension. Pictorial items appear in human intelligence tests as early as 18 months, suggesting that this should not be considered a particularly difficult skill. Nevertheless, Viki made many mistakes, and it would be interesting to know what caused them.

If we pool the data for realistic, colored pictures from discrimination groups A and C and matching groups E and F, we find that errors occurred on 11 per cent of these 168 trials, which would be expected if 22 per cent of the responses were pure guesses. This may be interpreted as indicating that Viki could not identify the objects illustrated in 22 per cent of these trials; however, we have been unable to find any characteristic of the missed pictures which would appear to make them more difficult than the others. An alternative interpretation would be that the errors were due largely to careless responses—which is consistent with our observation that Viki often chose very quickly, after only a brief glance at the pictures. It should be noted that our procedures, which utilize a new pair of stimuli on each trial, are more demanding of precise perception than are the customary discrimination and matching procedures, which require only the recognition of familiar stimuli. The significant difference between colored and black and white pictures in group C of the discrimination experiment does not distinguish between these interpretations, since colored pictures may be thought of as having more realism, or more attention value, or both.

In the generalized discrimination experiment, we attempted to eliminate consistent form cues from the pictures; however, if our efforts are assumed to have been inadequate, our results may be ascribed to generalized form discrimination, which could have occurred even if the pictures were not functioning as representations of real objects. In the generalized matching experiment, however, it would be necessary for the *S* at least to see the relationship between the form of the three-dimensional sample and that of the corresponding two-dimensional picture—which is perhaps the least that can be meant by "picture perception." The comparison of picture discrimination with nonsense design discrimination provides further evidence that pictures actually serve as representations for this *S*: If the pictures had been perceived merely as colored forms, they would probably have been more difficult than the nonsense designs, since the latter were characterized by simple and obvious differences in color as well as form and size.

Our results indicate that pictorial representation is a usable channel for communication from man to chimpanzee. It does not follow, of course, that this medium can be used by chimpanzees to transmit information to men or to other chimpanzees. (At five years of age, Viki's "drawings" contain nothing which we have been able to recognize as representations.)

SUMMARY

The picture perception of a home-raised chimpanzee is evaluated in terms of imitation, discrimination, and matching experiments, as well as observational data. The results indicate that the *S* recognizes a large proportion of what she sees in pictures, even at the level of abstraction of black and white line drawings.

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PERCEPTUAL DIFFERENTIATION AS A FUNCTION OF NONDIFFERENTIAL REWARD AND PUNISHMENT

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In a recent study Bitterman, Calvin, and Elam (1) investigated the effect of nondifferential reward at two points on an afferent dimension upon the rate at which a discrimination between those points was subsequently learned. Three groups of rats were trained in a two-window jumping apparatus. In the first stage of the experiment, during which all responses were reinforced, one group jumped to each of a pair of identical mid-gray cards, a second to horizontal and vertical stripes presented in simultaneous configurations (horizontal-vertical and vertical-horizontal), and a third to the horizontal and vertical stripes in successive configurations (horizontal-horizontal and vertical-vertical). In the second stage of the experiment all animals were trained on a horizontal-vertical discrimination, half of each group on the simultaneous problem and half on the successive problem. Contrary to expectations based on the concept of a negatively accelerated growth of habit strength as a function of reinforcement (2, 3, 4), the performance of the animals pretrained on gray cards was not superior to that of the other two groups. The data suggested instead that a considerable amount of perceptual differentiation may develop in the course of nondifferential reinforcement.

The experiment to be reported here was designed to compare the effects of nondifferential reward and punishment. Since it was considered probable that nondifferential punishment introduced in the course of an experiment like the first would constitute a no-solution problem and produce obscuring emotional reactions, a new method was devised. Nondifferential reward and punishment on horizontal and vertical stripes were given in the context of a problem to the solution of which the horizontal-vertical difference was irrelevant. In the previous experiment perceptual development in the course of nondifferential reinforcement was configurational in character; positive transfer was largely limited to the groups which were pretrained on stripes presented in the same configurations used in the test problem (i.e., simultaneous-simultaneous and successive-successive). Since the pretraining and testing configurations differed in the present experiment, there was some doubt as to whether positive transfer would be found; but the possibility was considered that the introduction of a problematic context would significantly facilitate perceptual differentiation. Nevertheless, the main purpose of the experiment was to inquire into the effects of nondifferential punishment.

METHOD

Subjects

Forty naive albino rats, bred in the laboratory from Wistar stock, were studied. The animals were between three and four months old at the beginning of the experiment.

Apparatus

A conventional two-window jumping apparatus of the kind devised by Lashley was employed for the experiment. Behind the windows was a feeding platform, and below them was a cloth net into which the animals fell after incorrect responses. The entire apparatus was mid-gray in color. Four stimulus cards were used, one black, one white, and two black-and-white striped cards (stripe width = ½ in.) of which one was horizontally and the other vertically striped.

Preliminary Training

All animals were maintained on a 24-hr. feeding schedule throughout the experiment. After being fed on the feeding platform for several days, they were taught to jump gradually increasing distances (up to a maximum of 9 in.) through the open windows. Each jump was rewarded with a nibble of wet mash.

Experimental Design

The design of the experiment, which was divided into three stages, is illustrated in Table 1. In the first stage of the experiment, all animals learned a simultaneous black-white discrimination, half the animals being trained on white-positive and the other half on black-positive. Training was by the correction method. Each trial consisted of a series of jumps terminating in a correct response. The animal was allowed a maximum of three free jumps to a given pairing of the stimuli, and after three successive errors it was guided in the

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EFFECTS OF PRETRIAL IMMERSION ON MAZE PERFORMANCE OF RATS: I. A ONE-CHOICE MAZE[1]

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A major concern in animal psychology is the efficiency of motivating factors as measured by the animals' accomplishments on problems given them by the investigator. While there is no approved method of assessing "wastage" of motivation in general, there is no lack of agreement with the simple assertion that much of an animal's effort in problem solving is fruitless under laboratory conditions. The wastage is roughly analogous to that of combustible gases and carbon that "go up in smoke" from a coal-burning engine operating at full draft but converting into useful kinetic energy only a small fraction of the potential energy of the coal it consumes.

Frequently, in laboratory settings, low efficiency of motivation is associated with pretrial conditions that arouse hyperactivity, as when animals are enraged or emotionally aroused by severe threat of punishment; also, with conditions that curtail activity or variation of attempts, as in the timid, cowed, or confused *S*. Contrariwise, high efficiency often attends those efforts that are characterized by calmness, variation of attempts, relevant use of prior habits, desistance of unproductive acts, and unification of responses which by accident or insight led to mastery of the problem. Thus, within limits, an *E* can crudely assess the efficiency of motivation by the accomplishments of the animal, despite the pitfall of circular reasoning this procedure entails.

In recent years many reports have been published in which what appeared to be "strong" motivation proved actually to be relatively low efficiency, as measured by accomplishments in problem solving (4, 6, 7). They are exemplified by the maze study of Mason and Stone (5) on rats which were required to swim underwater from start to goal. The necessity of holding its breath agitated the rat and increased fruitless struggling. Learning rate was significantly poorer than that of the controls swimming leisurely on the surface and without any threat of anoxia.

To discover additional conditions in which the efficiency of motivation is relatively low, and also ways of improving its efficiency, a series of maze studies is in progress in which total immersion is imposed on rats just before each trial proper begins. The pretrial immersion is of sufficient duration to arouse panic-like hyperactivity but, at the same time, is without danger of drowning the animal. This method enables one to contrast the efficiency of a panic-arousing experience at the start of a trial with that afforded by the usual, immediate release of rats on the surface or with only momentary "dunking" to start them on their way.

METHOD

Apparatus

In the first of the immersion studies to be reported a one-unit water maze was used; its pattern and dimensions are shown in Figure 1*a*. All parts of the maze are constructed of galvanized sheet metal. It was placed in a small tank where the depth of water was maintained at approximately 8 in. The starting cage is shown in Figure 1*b*. It is made of hardware cloth but has a solid door to close the exit and also to prevent reentering the starting well. It serves as point of departure for both groups but also serves as immersion cage for the experimental group.

Subjects

Fifty male albino rats approximately four months old and roughly matched in control and experimental groups began the experiment. One *S* of the experimental group died. All were tame but without previous training on instruments. Their average weight was 226 gm. Since we relied upon "escape from water" as the primary motivating device, no change in the dietary program was required. Eleven pairs (experimentals and controls) had only 25 trials.[2] Fourteen controls and 13

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[1] This study was supported by the Scottish Rite Fund for Dementia Praecox Research, New York City, to which grateful acknowledgment is made.

[2] The first phase of this study involved only 11 immersed and 11 control rats. The formal training of the groups was terminated after 25 trials, but further work was done with a few rats which had made no progress in choosing the correct turn. The results from these prompted the second phase of the study in which 14 pairs of rats were started.

experimentals had a total of 100 trials. For both groups the left turn was correct for trials 1 to 25. The groups receiving 100 trials had the same turn for the next 25 trials (26 to 50). For trials 51 to 75 their goal-ramp was shifted to the right side, and for trials 76 to 100, back again to the left position. The object of the shifts was to compare the immersed and the controls in respect to readiness (plasticity) to alter the directions of their turns when prompted by a change of the goal position.

Procedure

Preliminary training. To acquaint the animals with swimming, some practice in a 10-ft. straightaway was provided. Those destined for immersion were submerged in the starting cage for 30 sec. before release. The controls were released immediately as the starting cage was allowed to settle down in the water. At most they had no more than 1 or 2 sec. of total immersion. Both groups were free to swim on the water's surface although nothing prevented their diving and progressing beneath the surface.

In groups of four or five, each rat, in its turn, was given five trials per day for a total of five days. From 5 to 10 min. elapsed between trials, when the animals were kept in a warm container (c. 75°F.).

Maze training. On the sixth day maze training proper began. Groups of four or five rats swam in rotation as in the preliminary trials for a total of five trials daily. The experimental animals were immersed for 30 sec. before being released in the starting cage. Most of them surfaced immediately after the door of this cage was lifted. The control rats were "dunked" only momentarily as the starting cage settled into the water. They usually left at once, as did the experimental group, but sometimes paused, "straddling" the alley before departing.

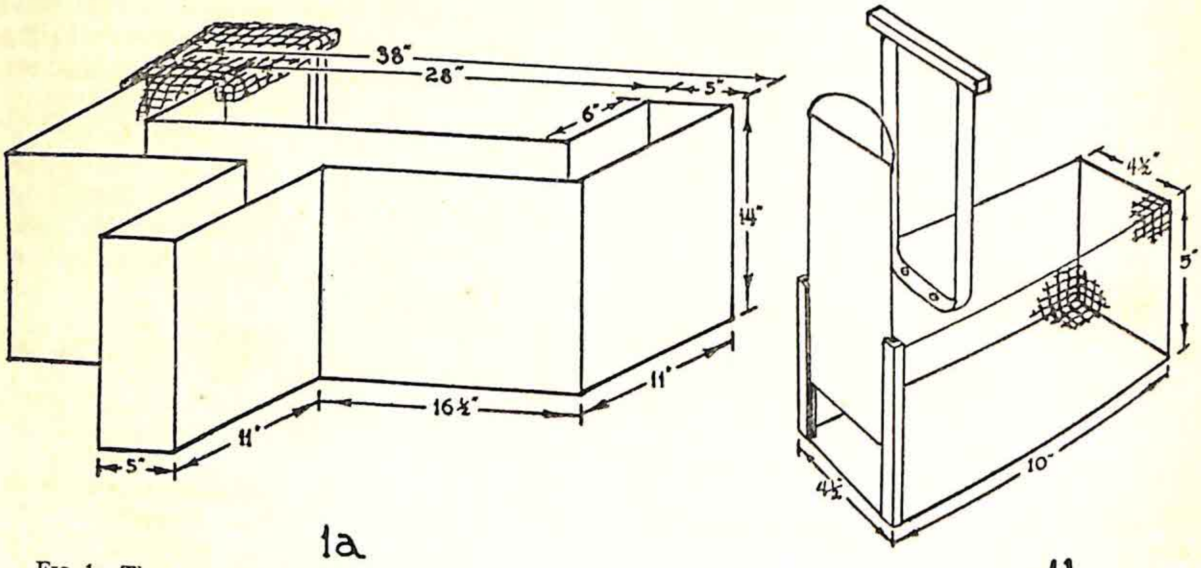

FIG. 1*a*. The single-unit U-type water maze; Fig. 1*b*. Starting cage serving as portal of exit for both groups and for immersion of the detained group

RESULTS

Some qualitative remarks concerning the responses of the animals are appropriate although none of the responses seemed worthy of quantification at the time of the experiment. On the first preliminary trial most of the control and immersed rats alike made vigorous efforts to escape by force from the starting cage as it sank into the water. When the door was raised, some were so preoccupied elsewhere, or confused, that they failed to orient properly to the opening. On subsequent trials, however, appropriate orientation soon occurred in the controls, but some of the immersed rats continued to exert great effort at the wrong places for a long time. Several of them soon began to crouch, motionless, for the first 10 to 15 sec., and then to resume frantic efforts to escape by clawing, biting, and pushing during the remainder of the detention period. These responses were prevalent in the immersed group. Some of the latter swam a portion of the straightaway underwater. Subsurface swimming did not carry over to the maze, however, probably because the alley wall was directly in front of the door of the starting well.

"Straddling" in the alley was done frequently by a few animals of both groups. While straddling they turned the head from side to side or looked backward before moving on. No characteristic difference in rate of mastery was noted between those *S*s in which straddling was frequent as compared with those in which it was rare. Quite probably this is a simple defensive act which enables the animal to pause without sinking low in the water.

Error Data

Error graphs depicting differences in trends between controls ($N = 25$) and immersed animals ($N = 24$) for trials 1 to 25 are plotted in Figure 2*a*. Retracing errors were rare in this phase of the learning and have no differentiating value; hence, the graphs were based on only the blind alley entries. For trials 1 to 25 the means of total errors for controls and immersed animals are 5.6 and 12.6, respectively. As indicated by *t*, the difference is significant at the .001 level.

Figure 2*b* is based on wrong choices by the 14 control and 13 immersed rats which continued through 100 trials, as specified earlier. It is plotted as a continuation of the data for trials 1 to 25 because there was, in fact, no change in conditions through trials 26 to 50. The upward shift in means for the immersed group results from dropping the 11 rats which, as a group, were slightly better than the remaining rats. As is apparent, the controls continued with only occasional errors, and the immersed rats, as a group, made very gradual improvement. Two immersed rats never varied at all from the "stereotyped," wrong choices already apparent during trials 1 to 25. They swam down the wrong alley, whirled about, swam rapidly back to the goal-end with such unity of action that to an observer the apparent intent was no less clear-cut than that of immersed rats making correct turns. While not conforming to the *E*'s definition of right choice, these responses were executed with about the same degree of automaticity as technically correct choices.

Figure 2*c* is presented as a continuation of 2*b*, although in one important respect it actually was not. Before trial 51 the *E* shifted the goal-ramp from left to right side. Thenceforth, by definition, left turn was wrong and right turn correct. The graphs clearly indicate a difference in the lability of habits of the control and immersed groups. All the controls made mistakes at first, as one would forecast because of their previous mastery of the problem; but within a few trials correct choices began to appear within this group. None shifted abruptly and, as usual, some shifted earlier and more consistently than others; hence the daily means fall off gradually as shown in Figure 2*c*.

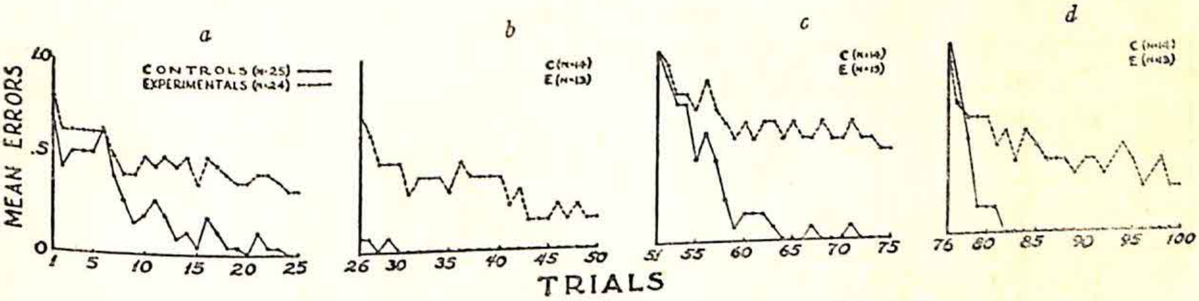

FIG. 2*a*, *b*, *c*, *d*. Error curves for successive groups of 25 trials

The individual records of the immersed animals differ markedly from those of the controls. Two rats that had always turned (erroneously) to the right continued to do so, but did not exit on arrival at the ramp; instead, they spun around like robots and swam back promptly to the left end without displaying clear-cut evidence of having noticed the ramp. They made several back-and-forth excursions before using the ramp on trial 51. Five immersed rats which had learned to turn to the left on trials 1 to 50 continued to make the same turn during trials 51 to 75. This is one of the most striking differences between the immersed and the control animals; the latter adapted to the change of goal position rather promptly, whereas the former perseverated in the previously correct choice. A latent tendency to perseverate is the essence of the difference between the correct-responding rats of the control and the immersed groups on trials 51 to 75. In retrospect it provides what justification one has in speaking of normal overlearning in the controls and "stereotypy" or "fixation" on the part of the immersed.

Figure 1*d* represents the error records for trials 76 to 100, when the ramp was again back on the left, where it had been for the first 50 trials. As on trial 51, the controls uniformly started with the maximal number of errors, and the immersed, as individuals, did just what they had been doing before, whether right or wrong. Those that had never made any but the right-side choice, as well as those that had learned to turn right during trials 51 to 75, made wrong turns on trial 76, whereas those that had made left choice (erroneously) throughout trials 51 to 75 now were right by accident.

Soon after the goal shift was made (trial 76), the controls began turning to the left, and with but two exceptions were always turning correctly by the end of the first day. No immersed animal that had learned the correct turn in trials 51 to 75 mastered the left turn during trials 76 to 100, although three of them began to vary their choices and thereby showed promise of ultimate mastery with further trials. Three rats never made a correct turn; four were always right simply because they had never ceased to take this turn after it was mastered during trials 1 to 50. Again, as on trial 51, the immersed rats that suddenly became correct-choice animals, because the ramp was shifted, appeared to ignore the ramp on arrival at the left end of the main unit. They whirled automaton-like and shuttled back to the other end as they had been doing. After from one to five excursions they used the ramp and continued to do so on subsequent trials without delay.

DISCUSSION

Gilhousen (2), in experiments showing that rats would "fixate" a complicated pathway involving a series of jumps to food when a more direct pathway was available, is sometimes credited with being the first to isolate the concept of "fixated" behavior in rats. Phenomena somewhat remindful of these had already been discussed in earlier studies dealing with tenacious position habits occurring in discrimination studies and persistent errors that stood out against mastery of certain types of mazes. Recently, interest has centered largely on the relation of certain "psychological" states, such as intense hunger, confusion, frustration, anxiety, etc., to the occurrence of stereotypy and perseveration of maladaptive responses.

In the present study, panic-like hyperactivity was aroused in the immersed rats before each trial. In respect to curtailment of individual variability of attempts, the effect was somewhat like that reported by Elliott (1), who found that as hunger increased in intensity, variability of response appeared to be curtailed in his fan-shaped maze. Unlike the study of Krechevsky and Honzik (3), however, the lack of docility in transfer situations appears not to be attributable to overlearning per se, because the habits of the controls were very labile despite a great deal of repetition of one type of response. The no-solution situation used extensively by Maier (4) and co-workers as a means of arousing frustration hardly warrants aligning our results with theirs because the essential problem in the present study can be solved so readily at any time. However, the contrast between labile and "fixated" responses is a prominent feature of both studies.

At present our primary concern is with efficiency and inefficiency of motivating the rat to choose the shortest route to the goal. Mason and Stone (5) showed that surface swimming was superior to enforced underwater swimming in promoting choice of the shortest route. The present study shows that immersion for 30 sec. just prior to each trial is relatively inefficient as compared with release with only momentary "dunking." Studies in progress suggest that the experience of immersion, as opposed to the 30-sec. delay at the start, quite probably causes the relatively poor records of the immersed rats. Other variables still have to be investigated, however, before one can say with conviction which factors are, and which are not, causal in promoting the efficient mastery of a simple maze. For example, there is evidence that a rat immersed for 30 sec. will master the one-unit maze and transfer when the goal is shifted just as rapidly as its control if the wrong alley is covered with transparent Plexiglas that forces underwater swimming. Also, when immersed rats are required to swim down a straightaway for a short distance (3 ft.) before making the choice, they master the choice at the same rate as their controls. Possibly, even a few seconds' detention after immersion would accomplish the same result as swimming for 3 ft., but this variable remains to be tested, as do also other seemingly trivial factors that may contribute significantly to the efficiency or inefficiency that characterized the groups of this study.

Some of the foregoing devices may be no less effective in breaking up "stereotyped" choices than in their prevention from the outset. Investigations along lines of correction as well as prevention are contemplated.

SUMMARY

The present study deals with pretrial immersion that causes low efficiency in rats' learning a one-unit water maze, efficiency being indicated by the rate of mastering the most economical route to the goal. It also deals with the unadaptibility that limits the animals' success in modifying their habits as required in transfer problems. Points that bear most interestingly on the efficiency of learning and lability of habits in transfer problems are as follows:

1. Stereotyped, fixated behavior occurred in most of the immersed animals; in consequence, their rate of progress in mastering the left turn during trials 1 to 50 was significantly inferior, as a group, to that of the controls. Two of the 13 immersed animals never made a correct response.

2. Long repetition of right choices (overlearning) by the controls was not associated with loss of adaptability in the transfer situations. However, stereotyped, fixated behavior characterized the immersed rats that made correct turns from the beginning or which learned to do so in the 50-trial series; it was evidenced by failure or by greatly retarded shift of choice following transfer of the goal-ramp to the opposite side.

3. The immersed rats that had always swum to the right side (erroneously) in trials 1 to 50 failed to use the ramp immediately after it was shifted from left to right; instead, they swam to the right end, whirled around, and then swam directly back to the left end (now wrong), suggesting that the entire series of movements was well integrated. After one or two trials they used the ramp on arrival at the right side.

4. Exploratory experiments indicate that small changes in the experimental setup are effective preventives of stereotyped, fixated behavior in immersed animals. Further study of both preventive and corrective devices should prove to be enlightening.

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ADDITIVITY OF CUES IN VISUAL PATTERN DISCRIMINATIONS BY MONKEYS[1]

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This experiment was designed to determine the relative discriminability of pattern stimuli which differed in color (C), form (F), or size (S) alone, or in the four possible combinations of these variables, i.e., color and form (CF), color and size (CS), form and size (FS), and color, form, and size (CFS).

Learning theorists of the S-R school (2, 5) have explicitly or implicitly predicted that learning is more rapid when relevant stimuli are presented in more than one modality. This prediction has been confirmed experimentally (1, 8). S-R theory is, however, vague concerning the possibility of, or the effects of, additivity of cues from different stimulus dimensions within the same modality. Hull's (6) postulate of afferent neural interaction is obviously concerned with these relationships, but at the present time is quantitative only with respect to external inhibition and external inhibition of internal inhibition (6, pp. 94–95).

The lack of more precise expression is doubtless the result of an absence of major quantitative studies. These experiments are needed to demonstrate the size of the effects, the relations among qualitatively different dimensions, and the characteristics of the compound effects.

METHOD

Subjects and Apparatus

The complete experimental history of the seven rhesus monkeys (No. 156, 157, 158, 159, 160, 162, and 164) which served as *S*s in this study has been reported in a previous publication (11) except for 20 days' testing on patterned size discrimination problems (13), which intervened between the conclusion of the experiment cited and the beginning of the present study.

The basic test equipment was the Wisconsin General Test Apparatus (4, Fig. 1).

The stimuli were 210 pairs of geometrical figures cut from colored construction paper and mounted on 3-in. by 3-in. squares of white posterboard. Each pair of figures varied in color, form, size, or in the four combinations of these variables taken two or three at a time. Those stimuli which varied in one or two categories were constant in the other dimensions.

The stimuli in the categories which did not involve size differences (C, F, CF) were figures with an area of 2.7 sq. in. The areas of the two figures in the categories which varied in size (S, CS, FS, CFS) were always 1.8 and 3.6 sq. in. Thus, the larger stimulus was 100 per cent larger than the smaller in these four categories, and the areas of both figures in the problems with size constant were intermediate to prevent transfer between these classes of problems. From ten different forms (cross, square, circle, triangle, rectangle, diamond, quadrant of a circle, semicircle, rhombus, and trapezoid) and ten colors (orange, red, black, yellow, yellow-green, brown, blue, green, purple, and gray), paired comparisons were formed by drawing two colors or forms at a time from these populations. The number of possible problems within the various categories was large, ranging from 100 to 2,025. Samples were taken at random from these pools of possible problems, and no particular paired combination of stimulus attributes was repeated during the experiment. Obviously, none of the populations of problems was exhausted.

Procedure

The individual trial procedure was the same as that previously described (12), and is standard at the Wisconsin laboratory.

Seven ten-trial problems, one within each of the stimulus categories, were tested each day for 30 days, a total of 210 problems. Within each category the (+) and (−) designations were randomized so that no color, form, or size was consistently rewarded or nonrewarded.

Experimental Design

In order to estimate the significance of learning and to remove temporal variations from the analysis of variance, the results were arbitrarily divided into six five-day problem blocks. This variable was included in a three-factor factorial design, with stimulus categories and individual monkeys as the other two independent variables.

RESULTS

The analysis of variance, summarized in Table 1, indicates that individual differences and stimulus categories are significant at the .001 confidence level. The *F* value for problem blocks is significant at the .05 level of confidence. The interproblem learning curves, however, are irregular and give little evidence of consistent improvement with practice.

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[1] This experiment is part of a dissertation conducted under the direction of Professor Harry F. Harlow and submitted in partial fulfillment of requirements for the degree of Doctor of Philosophy in the department of psychology at the University of Wisconsin in 1953.

[2] Now at the University of Oregon.

The classes of stimuli may be divided into two groups on the basis of errors made on trials 2 to 10. Performance on the categories involving color differences was consistently superior, by 12 to 17 per cent, to performance on those categories which did not differ in color (CFS, 6.6 per cent errors; CF, 7.6; CS, 8.5; C, 8.9; FS, 20.7; F, 22.7; S, 25.5). Tukey's (10) gap test indicates that C, CF, CS, and CFS constitute a homogeneous group of categories, that performance on these categories was significantly superior to performance on F, S, and FS, and that none of the differences among the latter three classes was significant. The more lenient *t* test of related measures indicates that FS was superior to F ($t = 3.07$, 6 *df*) and to S ($t = 2.64$, 6 *df*) at the .05 level of confidence.

TABLE 1

Summary of Analysis of Variance

SOURCE	*df*	MEAN SQUARE	*F*	*p*
Monkeys	6	301.45	49.74	.001
Problem blocks	5	32.41	5.35	.05
Stimulus categories	6	576.99	95.21	.001
M × PB	30	10.50	1.73	
M × SC	36	14.55	2.40	
PB × SC	30	13.34	2.20	
M × PB × SC	180	6.06		
Total	293			

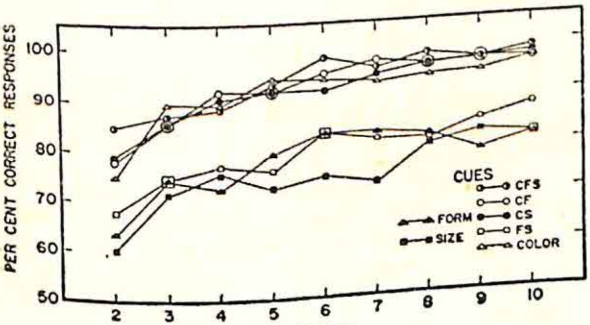

FIG. 1. The effect of combined stimulus cues on intraproblem learning

The intraproblem learning curves presented in Figure 1 show more clearly the precise effects of stimulus dimensions on discrimination learning. The intraproblem curves for the categories which include C (color) differences all have a much higher slope constant and asymptote than the curves derived from F, S, and FS discriminations. The addition of F, S, or FS dimensions to C does not change the asymptote, but there is a greater discontinuity at trial 2 (i.e., fewer errors) and a more rapid approach to the asymptote on succeeding trials. Comparison of the FS curve with the F or S discrimination learning curves reveals similar differences.

DISCUSSION

The results of this experiment are in good agreement with previous studies of the relative discriminability of stimulus dimensions in monkey and man. Harlow (3), Meyer and Harlow (9), and Warren and Harlow (14) found color a more easily differentiated discriminandum for monkeys than form or size. Stimuli which differed in form and color were little, if any, more discriminable than those differing in color alone.

The great superiority of C over the F and S categories shows clearly that color is a prepotent cue in the discrimination learning situation. The dominance of color is reflected in the findings that performance is not significantly improved when form or size differences are added to color. This finding corroborates Lashley's (7) concept of perceptual dominance.

The results of this study provide some evidence for the additivity of cues in the discrimination learning of monkeys as indicated by the differences in the intraproblem learning curves when single and multiple stimulus dimensions were employed. Fewer errors were made on the combined FS discriminations than on the discriminations differentiated by only the F or S dimensions, and this difference approached statistical significance.

The data of this experiment agree with those of earlier experiments in indicating that little or no gain is obtained when additional cues are added to highly effective single-dimensional cues, specifically, color. Two relatively ineffective single-dimensional cues, as form and size, may produce facilitative effects when co-joined, but even here the differences are not great. The performance increment is certainly not algebraical under any circumstances and has not yet been reduced to any precise mathematical function. Although the data of this experiment and related experiments emphasize the importance of dominance, they are not opposed to the principle of additivity of cues, particularly of those whose dominance is low.

SUMMARY

Seven rhesus monkeys were tested on 210 pattern discrimination problems which differed in color, form, size, and all possible combinations of these three variables. Color-difference category differed significantly from any other in facility of solution, and performance on all color-difference categories was significantly better than on those which differed in form or size or both form and size. The form and size category was more discriminable than form or size alone.

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THE SPECIFICITY OF THE FIXATED RESPONSE IN THE RAT[1]

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Maier and his students have shown that subjecting rats to frustrating insoluble problem situations leads to rigid, stereotyped behavior that persists even when solutions are later made available (3). They have also shown that manually interfering with fixated rats' responses by forcing correct responses caused the rats to abandon their fixated responses and solve the problem. This procedure, designated as "guidance," consisted essentially of trials in which the *E*'s hand was placed next to the rat to prevent a response to the wrong window and the rat was nudged to the correct window. Maier and Klee (7) made a detailed study of the role of guidance in the alteration of abnormal fixations to find the most effective means of application and the mechanisms governing the resultant behavior changes. They compared two techniques by which learned and frustration-instigated responses were altered and adaptive responses learned in new soluble problem situations. These were (*a*) by ordinary trial-and-error learning, and (*b*) by guidance (i.e., forcing the animals to make correct responses) on some of the trials in the new problem. They found that when guidance was used, the old responses were consistently altered, permitting the new problem to be mastered. They also found that when guidance was given on every other trial, almost every rat was able to abandon its previous responses and learn the new problem.

In this study, an apparatus was designed which permitted fixated animals to walk on a runway to the correct window on alternate trials. If the significant features of guidance are prohibition of the fixated response, escape from punishment, reward of food, and the experience of responses made on the basis of discriminations to be mastered, then this technique would also break fixations. If fixations are not altered by this method, the above factors would be ruled out, and other mechanisms would have to be proposed and tested.

There are also available from this technique significant data concerning the controlling stimuli of fixated responses. If the animal is fixated to some specific stimulus *object* in the jumping situation, one would expect to observe similar types of fixated behavior in the walking situation. On the other hand, if the fixation is a response in a specific *situation*, one could expect few similarities in performance during jumping and walking trials. Thus, the problem is also one of determining whether the fixated response is a specific response in a specific situation, or whether it is a response which is governed by a limited stimulus area of the situation.

METHOD

Apparatus

A modified Lashley jumping stand was used in this study (1). This apparatus consists principally of a jumping platform situated 8½ in. in front of two Plexiglas windows 6 in. square. Projectors threw an image of a black circle 8 cm. in diameter on a white field (Bw) on one window, and a white circle 8 cm. in diameter on a black field (Wb) on the other. Behind the windows was a food station. The rat was required to jump from the jumping platform to one of the windows. If it jumped to the correct window, the window opened and the rat received a food reward on the food station. A response to the wrong window resulted in a bump on the nose and a fall to a net located 4 ft. below the windows.

Connected to the front edge of the jumping platform was a V-shaped runway, each leg of which was 2 in. wide and reached to the windows when placed in position. The entire runway mechanism could be fastened under the jumping platform so that no part of it could be used by the rat while making a jumping response.

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[1] This research is part of a thesis submitted in partial fulfillment of the requirements for the Ph.D. degree at the University of Michigan. Appreciation is expressed to Norman R. F. Maier, the thesis director, for his patience and counsel, and for opportunities in his laboratory which led to this research. The complete thesis, "The Relationship between Guidance and the Specificity of the Fixated Response in the Rat," is available on microfilm from the University of Michigan, Ann Arbor, Mich., Publ. 2403.

Part of the experimental technique and results are illustrated in the film, "Frustration and Fixation," by R. S. Feldman and P. Ellen, available from the Psychological Cinema Register, Pennsylvania State College, State College, Pa., PCR-2034.

Preliminary Training

The training period was begun by placing the animals with their daily food ration on the feeding platform of the jumping stand. When the rats were eating well, trials were begun in which the jumping platform was moved to a position close to the windows and the rats were required to step from the jumping platform through open windows to the feeding station beyond. Each rat was given 10 trials per day. At every even-numbered trial the animal was guided to the window opposite the one it had chosen on the preceding trial. In this way each rat received 5 trials to each window. This procedure was designed to prevent position preferences during this stage. Every day the jumping platform was moved back about 1 in. farther from the windows so that at the end of approximately one week, the rats were jumping the complete distance of 8½ in. Next, the windows were gradually closed, with the result that the rats, after first brushing past them, eventually had to push them open to gain access to the feeding platform. The Bw and the Wb images were reversed on the windows before every odd-numbered trial, while the free and guided jumps were continued as before. This allowed each rat to jump to each side and to each window the same number of times in the training period.

After the rats were jumping readily through the windows, they were given a training series of 40 trials (10 trials per day) under actual experimental conditions. During these trials the rats were allowed 30 sec. to make a response. If the rat did not respond within this period, an electric "wand" was applied to its tail about twice per second until a response was made. Moreover, if the rat responded to the same position or the same window (Bw or Wb) three times in succession, it was guided to the opposite side or window. The rats were then ready for experimental procedures.

Experimental Procedures

Stage 1: The nonsolution stage. The first step involved frustrating the animals to produce the stereotyped responses which previous studies had frequently shown to be fixations. Therefore, the animals were placed in an insoluble problem situation in which the windows were locked and the stimulus patterns interchanged in a set, random order so that the rats were successful only 50 per cent of the time no matter which side, or window (Bw or Wb), or consistent combination of these was chosen. In this study all animals were frustrated for 160 trials. A study by Maier and Feldman (4) indicated that this number of frustration trials was sufficient to produce an optimum number of fixations. All rats were stimulated with the electric "wand" if they hesitated more than 30 sec., and the latency of response was recorded after each trial.

Stage 2: The soluble problem stage. After 160 trials of random punishment, the rats with position responses were given a soluble discrimination problem (the Bw window was positive), and the rats that had a persistent symbol response to the Wb or Bw window were given an opportunity to achieve 100 per cent success by reversing their discrimination to the Bw or Wb window, respectively. This stage continued for 200 trials unless the animal abandoned its stereotyped response and solved the discrimination problem at a criterion of three consecutive days with not more than one error. Any rat that solved the discrimination problem would be removed from the study since only rats with demonstrated fixations were to be used for succeeding procedures.

Stage 3: Alternated jumping and walking trials. The animals that did not solve the problem and had either a position or symbol fixation were given 200 alternated trial-and-error jumping trials and walking trials. The walking trials were those in which the runways were placed in position to provide a path from the jumping platform to either window. Preliminary studies revealed that the rats had a tendency to fixate walking responses that did not necessarily correspond to the fixated jumping responses; therefore, to insure mastery of the walking response, guidance was given during some of the walking trials to prevent walking fixations. When *E* guided the animal, he placed his hand beside the rat and prevented it from making an incorrect response, and at the same time he gently nudged the animal toward the correct runway. Guidance was given only when an animal appeared to be making the same walking error twice in succession on the same day. More specifically, if a rat walked incorrectly to the left on the first walking trial of the day, it was punished. If the rat started to walk incorrectly to the left again, *E* guided the rat to the correct runway on the right. If the rat walked incorrectly to the left, it would be punished again, etc. Guidance was given as long as it was needed, i.e., when the animals no longer made consistent errors indicative of walking fixations, guidance was stopped.

A walking trial was scored as incorrect if the rat extended its body in the direction of the negative window and removed its four feet from the starting platform. When this occurred, the animal was pushed off the runway to the net below or it was guided to the correct window. It should be mentioned that guidance was never given on jumping trials.

Subjects

A total of 20 hooded and albino rats was used in this study. However, one rat died during the experiment from a respiratory ailment, and one rat did not become fixated and was eliminated from the experiment. Therefore, complete data were obtained from 18 rats. Three litters were represented consisting of 7, 6, and 5 rats, respectively.

RESULTS

Frustration and Soluble Problem Situations

Of the 19 animals that completed the frustration trials (stage 1), 9 developed left- and 4 developed right-position responses, 4 animals responded consistently to the Bw window, and 2 responded consistently to the Wb window.

In stage 2, all animals were placed in a soluble discrimination problem. The 13 animals that developed position responses and the 2 animals that had consistently responded to the Wb window had to learn to respond to the Bw window. For the 4 animals that persistently responded to the Bw window in stage 1, the Wb window was now positive. The results showed that 8 of the 9 animals with left-position responses continued to make these responses in stage 2. The one animal that was different showed a departure from its stereotyped position response after 117 trials in the solution stage (stage 2) and exhibited signs of not being fixated. Since only definitely fixated animals were needed for further procedures, this animal was dropped from the experiment.

The four animals with a right-position response persisted in this response in stage 2. Two of the four animals with Bw responses persisted in this response, and two of these animals abandoned this response during stage 2—one adopted a left-position response and the other adopted a right-position response. Also, the two animals with the Wb response abandoned this symbol response and adopted left-position responses.

It should be mentioned at this point that the rats that formed position responses were given 50 per cent *random* punishment in stage 1 and 50 per cent *orderly* punishment in stage 2. However, the rats that formed symbol responses received 50 per cent random punishment in stage 1 and 100 per cent punishment in stage 2 because these latter animals had to reverse their responses in order to solve the problem. This point is important because Maier and Klee (6) found that the amount of punishment is a significant determiner of fixations, and some of the results reported here are interpreted in light of those findings.

At the end of stage 2, 18 rats had stereotyped responses that were designated as fixations since they were practiced in the presence of a soluble problem. To demonstrate that these stereotyped responses were compulsive in character rather than due to an inability to discriminate between the windows, an analysis of the latency of responses was made for all animals that had formed position responses in stages 1 and 2. The animals which practiced symbol responses in stages 1 and 2 could not be included in this analysis for reasons which will be evident when the nature of the analysis is explained.

In our analysis, the average latency of responses to the negative window and the positive window was compared on a daily basis. For example, if the 12 rats with position fixations jumped to the positive card five times each on a given day for a total latency of 840 sec., their average latency of response to this window per trial on that day was 14 sec.

The results of this analysis of stage 1 and 2 are shown in Figure 1. It can easily be seen that in stage 1, when punishment is given at random, the animals express no preference for either card. However, when the problem becomes soluble (stage 2), the animals manifest a distinct difference in their behavior to each of the windows. Above all, the results indicate that these animals were practicing a position response despite the fact that they consistently discriminated between the positive and negative windows. These results support Maier's finding that latency measures provide an index of learning which has taken place when conditions keep this learning from more concrete expression.

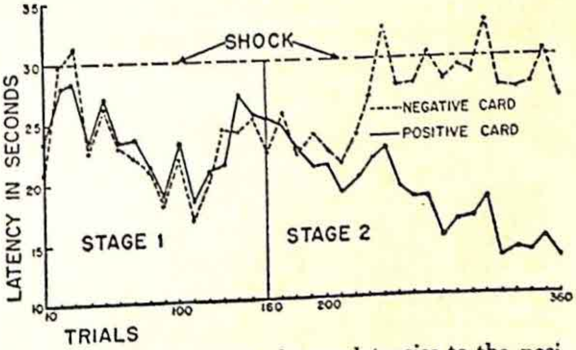

FIG. 1. A comparison of mean latencies to the positive and negative cards for rats with position fixations

The Effect of Introducing Alternated Walking Trials

In stage 3, all animals were permitted to learn to walk to the correct window. Attention is called to the fact that six of the animals which completed this stage had at some time manifested a symbol response. It is necessary to deal with these animals separately in the following analysis since, for varying periods of time, they had received 50 per cent more punishment than the animals with position responses. Maier and Klee (6) found that animals that had sustained 100 per cent punishment in being forced to reverse a discrimination or position response were more likely to become fixated than animals that had been subject to only 50 per cent punishment in being forced to change either from a position to a discrimination response or from a discrimination to a position response. If more punishment makes it more likely that a rat becomes fixated, it is also possible that these fixations will be stronger. And further, it is possible that the stronger fixations will generalize more readily to related situations. A separate analysis of the walking behavior of the 50 per cent punishment group and the 100 per cent punishment group provided evidence to support this possibility.

TABLE 1

Comparison of Guidance and Learning Scores between Position- and Symbol-Fixation Animals in Stage 3

	POSITION FIXATIONS (50% PUNISHMENT)	SYMBOL FIXATIONS (100% PUNISHMENT)	DIFFERENCE BETWEEN MEANS	t	p
Mean days of necessary guidance	7.4	12.1	4.7	2.32	$<.05$
Mean days needed to learn the walking response	10.9	15.3	4.4	2.00	$<.10$

The data show that all the animals that had position responses and had sustained 50 per cent punishment in stage 1 and 2 were able to satisfy the criterion of learning a correct walking response, viz., not more than one walking error in three consecutive days. Guidance was given for an average of 7.4 days, and the walking response was learned in an average of 10.9 days, not including criterion trials. Of the six rats that had symbol responses, two failed to satisfy the learning criterion in the 200 trials allotted for this test, although one of them achieved a perfect walking score on the last day of testing. In order to compare the walking behavior of the position-fixation and the discrimination-fixation animals, 20 days was assigned as the learning score since it would have been the minimal learning score that could be made by those animals that failed to satisfy the learning criterion. This arrangement of the data shows that these six animals as a group required 12.1 days of guidance and an average of 15.3 days to learn the discrimination response on walking trials. These results are shown in Table 1, and a comparison of the results of the two groups shows that the symbol-fixation group required nearly twice as much guidance and nearly one-half again as many trials to learn the walking response as the position-fixation group. The reliability of the difference was beyond the 5 per cent level of confidence. The difference between the mean number of days necessary to learn the walking response for the two groups was not reliable at the 5 per cent level of confidence. Although only one of these differences is significant, the direction of the differences is consistent with that obtained by Maier and Klee (6) in a study dealing with similar variables.

The Noneffectiveness of Correct Walking for Altering Jumping Fixations

The data showing the effect of correct walking responses on the stereotyped jumping responses in stage 3 revealed that in the 200 alternated walking and jumping trials no S was able to abandon the jumping fixation in favor of correct responses that were available to it during the jumping as well as the walking trials. This fact is significant, for 16 out of 18 animals had learned to make correct *walking* responses, yet they responded in a stereotyped and compulsive way to a position, or in terms of the negative window when they had to *jump* to the windows. It is further significant that in all the studies done by Maier and his students in which guidance was used to break fixations, it was rarely, if ever, found that a rat would persist in its fixated response after 200 alternated free and guided trials; yet, in this situation, walking responses instead of guided jumping responses on every other trial had no effect on the jumping fixation.

DISCUSSION

The principal results of this study indicated that frustrated rats that had fixated jumping responses persisted in these responses even when they had learned by some other means (walking) to make appropriate responses in the problem to be mastered. This means, first, that the effectiveness of the guidance technique used by Maier and his students does not depend in a significant manner either upon the mere absence of punishment and/or frustration, or upon the experience of success in some aspects of the problem to be solved.

Hilgard (2) has proposed that guidance brings back into the animal's behavioral field a cognitive appreciation that jumping to the alternative and the correct window is now a better response than its former stereotyped response that yields at best only partial success. Hilgard's conception of fixation holds that the rat persists in its stereotyped responses because it does not know that the conditions at the alternative window would be any better than those at the window to which it is responding at the moment. However, the data that are reported here refute this proposal inasmuch as it has been patently demonstrated that the animals will learn that the alternative position or card during walking responses is preferable and yet resist them when a jumping response is called for. Moreover, these data are in agreement with the observations made in Maier's laboratory of fixated rats' reaching toward the food cup and sniffing at it when it is in place just back of the opened window but refusing to jump to that position because of their compulsive attraction for the opposite position. Hence, it is unlikely that some simple cognitive mechanism is at the basis of the persistence of frustration-instigated behavior.

These data also bring into question the point of view that holds that compulsive behavior is the consequence of a breakdown of learning in the presence of anxiety. For example, in discussing human patients, R. W. White says, "The core of a neurosis lies at the point where anxiety has blocked or distorted the learning process so that the new learning essential to adjustment cannot take place" (8, p. 217). The evidence presented here fails to support the hypothesis of a "blocked or distorted learning process" since, unquestionably, learned discriminations between stimuli were found in our compulsive organisms both within the compulsive behavioral context (expressed as different latencies of response to the correct and incorrect windows) and closely related responses (in walking but not jumping trials).

On the other hand, another conclusion might be that the guidance technique does not seem to be effective unless the guided responses are of the same sort as those that are necessary for the correct execution of the problem. This conclusion may also be expressed as some failure on the part of the fixated animal to generalize between related stimulus complexes. It also seems evident that the fixated response is a specific response in a specific situation, for if the fixated response were merely the compulsive attraction for one window or position or a compulsive avoidance for the correct stimulus, it would seem that there would be a rapid generalization between jumping and walking responses, for position stimuli and the different windows were common to both conditions. An experiment to assess the extent of stimulus generalization between walking and jumping trials for normally trained animals would clarify this issue.

SUMMARY

Using a Lashley jumping technique, 20 rats were subjected to an insoluble problem situation for 160 trials. This resulted in behavior stereotypes which were found to persist during a subsequent soluble problem situation which lasted for 200 trials. The animals then were trained to *walk* along runways to the correct window on trials alternated with jumping trials. The results showed that while practically all animals learned to *walk* to the correct window, this learned response did not transfer to the jumping situation, and all rats persisted in their fixated responses. These results were interpreted to mean that one cannot account for fixations on the basis of a rat's having no reason to believe that alternative responses would be better than its stereotyped responses. Also, it is possible that the fixated response is a specific response in a specific stimulus situation, and that the animals were responding in terms of the whole situation and not to some restricted aspect of it, thereby reducing the possibilities for stimulus generalization.

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THE ABSOLUTE AND RELATIVE THEORIES OF TRANSPOSITION BEHAVIOR IN RATS

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Transposition is the name given to habit transfer between situations where the component stimuli differ but the relationships among the stimuli remain constant. Its theoretical importance is that it suggests a Gestalt or relational type of perceptual organization (6, 7) which conflicts with the neo-Pavlovian organization proposed by Hull (3) and Spence (8, 9, 10). The Gestalt-type and Pavlov-type theories of discrimination divide on numerous issues, but those portions of them which deal especially with transposition have been called the "relative" and "absolute" theories, respectively.

Stimuli lying along the dimension of visual size have, here, been selected to demonstrate the two theories, although any set of stimuli would have sufficed providing they could be ordered along a linear scale with regard to one feature, such as pitch or intensity. Suppose that there are three circles, one large, one medium-sized, and one small, which are, hereinafter, referred to by the letters A, B, and C, respectively. A rat is repeatedly given simultaneous presentations of A and B and trained, under conditions where size difference alone provides a differential cue, in the discrimination B(+) vs. A(−). The plus sign signifies approach and the minus sign avoidance. This pair is, now, replaced by C vs. B, and the rat is found to approach C spontaneously while B, approached during training, is no longer chosen. According to the absolute theory, this results from the rat's having acquired a stronger tendency to approach the specific stimulus C than to approach the specific stimulus B. Moreover, this difference of strength between the two tendencies is independent of the simultaneous presence of C and B. Any subsequent habit, therefore, which involved approaching C (or avoiding B) should be more easily learned than one which involved approaching B (or avoiding C). For the relative theory, the preference for C over B depends solely on the relationship between them, and if this is destroyed by presenting the circles in isolation instead of together, the one stimulus should be no more readily approached or avoided than the other. Suppose, then, that a number of rats are trained on B(+) vs. A(−) and show transposition to C vs. B. They are split into two groups, the first group being presented with C only and trained to avoid it, while the second is trained to avoid isolated B. The absolute theory expects the second group to learn more rapidly than the first, i.e., expects a quantitative difference between the group training scores. The relative theory expects no difference in ease of learning between the groups. These are the divergent predictions which provided the starting point for the present experiment. Before, however, being cast into concrete form, these group differences were translated into differences in the quality of individual performances. There were two reasons for this. First, the obtaining of reliable group differences might have meant working with more rats than laboratory conditions allowed. Secondly, the theories refer to *individual*, not *group*, behavior and ought to be tested, whenever possible, by the examination of individual behavior.

The transition from group to individual differences was effected as follows. After discrimination B(+) vs. A(−) is learned and transposition shown to C vs. B, we wish to know the relative ease of learning discriminations involving only B and those involving only C. Suppose that each of those two stimuli is presented alongside an all-black stimulus (hereinafter referred to as X) and that the discriminations in question are X(+) vs. B(−) and X(+) vs. C(−). Preliminary investigations revealed that the rat does not learn those habits so rapidly that a few training trials on the one cannot be alternated several times with a few trials on the other before mastery is complete. With such alternate training, the relative theory expects a more or less smooth reduction in error score until X is always chosen. The absolute theory predicts that, superimposed on this smoothly declining error score, is an alternating rise and fall—a rise during the learning of X(+) vs. C(−) and a fall when X(+) vs. B(−) is being learned.

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METHOD

Subjects

The *S*s were 15 male hooded rats. At the start of the experiment, they were about 44 weeks old and experimentally naive.

Apparatus

The discrimination was between two cards filling the windows of a Lashley jumping apparatus. The 6-in. square windows were separated by a ¾-in. wide wooden strip which, to prevent rats' catching hold of it and saving a fall, projected, wedgelike, 1.5 in. in front of the windows. The 4- by 6-in. wooden jumping platform was level with the base of the two windows and situated midway between them. The distance between jumping platform and window was variable. A canvas net 3 ft. below the windows caught the rat after it had jumped to an obstructed card.

The cards were of stout, mat black cardboard on which appropriate symbols, cut from white paper, were glued. Centered on the three cards, A, B, and C, were circles of radius 5.1, 4.05, and 3.2 cm., respectively. The ratio of areas C:B and B:A was 1:1.6. Other cards were either all-black or all-white. Cards were regularly replaced by fresh replicas to eliminate any incidental cues introduced either in their preparation or in their use. The jumping platform and sides of the apparatus were painted mid-gray. Thus, when in position, the cards appeared against a mid-gray ground. The roof of the apparatus was of transparent Perspex and formed the top edge of the windows so that there was no wall above the cards against which the rats could strike when their jumping became forceful.

Preliminary Training

The rats were tamed, adapted to a 22-hr. food-deprivation cycle for 7 days, and accustomed to eating on the feeding platform. Training then progressed through the following stages: stepping from the jumping to the feeding platform; jumping from the former to the latter as the gap between them gradually widened; jumping against and knocking over unobstructed all-white cards which, at first partly and later entirely, filled the windows. To prevent position preferences, systematic manual guidance was given so that each window was jumped through as often as the other. Preliminary training took 30 days by which time the rats were jumping across an 8½-in. gap to knock over an all-white card and gain food. After each jump (and after each successful jump in discrimination training), the rat remained on the feeding platform for 15 to 20 sec. in the presence of moist, mashed rat cake. Between experimental sessions, the rats were in their home cages with a plentiful supply of water but no food. Shortly after each rat's daily session, rat cake was placed in the cage for 90 min.

Discrimination Training

The "correction method" was used. To illustrate: suppose the positive card is on the right and the negative card on the left; the rat, placed on the stand, jumps to the left and falls into the net; it is returned immediately to the jumping platform; again, it jumps to the left and, again, is returned to the platform; its third jump is to the right and food. The cards retain the same positions throughout, and the whole series of jumps, terminated by a correct one, constitutes "one trial." This example would be recorded as "one trial and two errors." When a trial entails no errors, it is recorded as "correct."

Between one trial and the next, the cards were either replaced in the same positions or interchanged according to a prearranged random order based on Gellermann's series (2). When, after one or a few errors, the rat hesitated to jump, its tail was either pinched or compressed sharply against the edge of the jumping platform over which the tail hung. In a few days, tail-tapping was discontinued, and by the time critical training was reached, the rats would make many errors without any apparent weakening of their spontaneous jumping.

The discrimination to be learned was B(+) vs. A(−), i.e., against any preference for the larger circle. Each rat had 10 trials daily for the first 7 days. Thereafter, the number of daily trials was raised to 15, and training continued until 68 out of 75 consecutive trials were correct. On the day after meeting the criterion, each rat had 10 presentations of C vs. B with neither card obstructed, so that choice of either led to food. If the rat did not transpose (i.e., choose C) on 9 of those 10 trials, training was resumed on the following day with the number of daily trials now increased to 25. Four additional days of training were given, i.e., 100 trials. On the fifth day, and on each day thereafter until the rat began to transpose, transposition tests were made before the day's training was begun. Since, during these tests, the rats either transposed or jumped consistently to one side, three or four test trials sufficed to show which type of behavior was present. If it was a position habit, testing was carried no further, and training continued for another day; if it was transposition, testing was carried on for 10 trials. Only one rat transposed consistently on the first test series. The others required anything up to 195 additional training trials before transposing, and three rats did not transpose consistently at all. This confirmed the previous observation (5) that in rats, as well as in monkeys and children, transposition is, up to a point, strengthened by overtraining on the original discrimination.

Critical Training

There were four possible critical training series which featured alternating blocks of trials on discriminations involving C vs. X and B vs. X. Numbered

I to IV, they are shown in Table 1. Each block consisted of five trials. Any particular block appeared four times in the series containing it, so that critical training involved a total of 40 trials given on the same day. The position of X on successive trials during the first and third presentations of any block was *lrllr* and, on the second and fourth presentations, *lrrlr*. For 7 of the 12 rats which transposed, critical training followed immediately after the transposition tests, and for the remaining 5, it followed 1 hr. later. The presence or absence of the hour's interval did not appear to influence subsequent performance.

TABLE 1

The Four Critical Training Series

Series I	B(+) vs. X(−); C(+) vs. X(−); B(+) vs. X(−) . . . . . .
Series II	X(+) vs. C(−); X(+) vs. B(−); X(+) vs. C(−) . . . . . .
Series III	C(+) vs. X(−); B(+) vs. X(−); C(+) vs. X(−) . . . . . .
Series IV	X(+) vs. B(−); X(+) vs. C(−); X(+) vs. B(−) . . . . . .

TABLE 2

Scores on Discrimination and on Critical Training

CRIT. SERIES NO.	RAT NO.	DISCRIM. TRAINING		CRITICAL TRAINING							
		1	2								
I	1	190	390	2(14)	3(2)	2(3)*	4(1)	1(4)*	4(1)	5(0)	5(0)
I	2	310	410	2(10)	3(2)	2(5)*	4(1)	3(2)*	5(0)	4(1)*	5(0)
II	3	190	340	3(2)	5(0)	4(2)*	5(0)	4(2)*	5(0)	5(0)	5(0)
II	4	250	325	1(7)	1(4)	0(9)*	2(3)	2(3)	4(1)	1(7)*	4(1)
II	5	250	325	2(7)	4(1)	3(2)*	5(0)	2(3)*	4(1)	4(1)	5(0)
II	6	175	375	1(23)	3(2)	1(6)*	5(0)	3(2)*	5(0)	5(0)	5(0)
III	7	160	285	2(10)	2(7)	4(1)	3(4)*	5(0)	4(1)*	5(0)	4(1)*
III	8	285	435	3(2)	1(32)*	0(11)*	2(5)	2(3)	1(7)*	5(0)	1(4)*
IV	9	160	285	4(5)	3(2)*	5(0)	4(1)*	5(0)	5(0)	5(0)	5(0)
IV	10	400	400	3(10)	4(1)	5(0)	3(2)*	5(0)	5(0)	5(0)	5(0)
IV	11	220	395	1(6)	2(5)	4(1)	3(3)*	4(1)	4(1)	5(0)	3(2)*
IV	12	250	425	1(29)	1(20)	2(5)	0(10)*	5(0)	3(2)*	5(0)	4(1)*

Note: In "discrimination training" columns, the first score (column 1) represents the number of trials required to reach the learning criterion; the second score (column 2) represents the number of trials required before consistent transposition appeared. "Critical training" scores represent the number of correct trials (with, in brackets, number of errors made) on successive five-trial blocks; reversals are marked by asterisks. Series I and II present the more difficult discrimination (according to absolute theory) first, while Series III and IV present the easier discrimination first.

RESULTS

Rats No. 1 to 12

The performances of the first 12 rats are summarized in Table 2. In critical training, every rat had at least one reversal, i.e., had, on one block, more errors and/or fewer correct trials than on the immediately preceding block. There was a total of 28 reversals all of which, with but one exception, occurred where the absolute theory had predicted. Group results also support this theory. Altogether, there were 240 trials of either C(+) or B(−) and 240 trials of either B(+) or C(−). With the latter 240 trials (on the more difficult discriminations, according to the absolute theory), there were 134 (56 per cent) correct trials and 226 errors; with the former group of trials, there were 190 (79 per cent) correct and 104 errors.

Before these results can be unambiguously interpreted, two related difficulties must be disposed of. The first concerns the deduction from the relative theory of a smooth learning curve in critical training. Training alternately on two discriminations might, by itself, bring about unevenness in the learning curve, or unevenness might be present in any curve, even when only one discrimination was being learned. Of course, reversals produced in either way would have a random distribution so that, by itself, a possible alternation factor could not account for the systematic results obtained. It might, nevertheless, go some way toward explaining them. The second difficulty is that some factor, quite irrelevant to the present issue, might, either alone or in combination with the effects of alternation, lie behind the systematic reversals obtained.

The first difficulty can be settled by determining whether reversals are a necessary outcome of alternate training. Eight rats (no. 3 to 6, 9 to 12) were examined further on the two days after critical training. On those days, card X had ¼-in. wide stripes of white paper pasted along its two diagonals. This was to reduce transfer effects due to learning in critical training which had involved X. The four rats which, in critical training, had had series IV, had, on the first day, 20 trials on series I and, on the second, 20 on series IV. Likewise, the rats which had had series II were given 20 trials on series III and on series II on, respectively, the first and second days. In terms of the absolute theory, critical training might or might not have eliminated the strength difference between the tendencies to approach isolated C and isolated B, but it would have lessened the difference by having trained the rat to react in the same way to both C and B. The result would be a fairly smooth learning curve on each of the two further training days. Such, in fact, was the case. There was only one reversal in all 16 learning curves (one curve per day per rat). Neither did group results reveal any habit strength difference between the reactions to C and to B.

The second question can be answered if we know whether the distribution of reversals is susceptible to changes in the problem learned in discrimination training. Evidence on this comes from a preliminary study which used the same apparatus and comparable *S*s. To circles A, B, and C was added another of radius 2.55 cm. (card D) to form a series with the area ratios of D:B and C:A equal to 1:2.5. The training pair was C vs. A, the testing pair D vs. B. Transposition between two such pairs differs from the classical "one-step" transposition in which the pairs maintain the relationship between their members and possess one member in common, but, for present purposes, the complication of the overlapping pairs is irrelevant. Ten rats were trained in discrimination C(+) vs. A(−) and five on the reverse discrimination A(+) vs. C(−). When each rat had transposed appropriately to the test pair, its reactions to isolated D and B were tested by alternate critical training. In both groups, different strengths of approach tendency to the two cards were revealed by both individual and group results. But the group of ten showed the stronger reaction to D, while the group of five showed it to B.

Rats No. 13 to 15

These rats, unlike the first 12, did not show transposition when it was tested for but showed, instead, consistent position preferences. So their performances are not relevant to the immediate theoretical issue. It is noteworthy, however, that these rats were deviant in one other respect: they showed little VTE during training and none at all while being tested for transposition. This, in itself, could account for failure to transpose. No matter how different the habit strengths of the two cards, if each elicits approach and if the rat does not look at both before jumping, a consistent card preference cannot be expected.

DISCUSSION

The experiment's chief relevance for the study of discrimination behavior in rats is that it supports the absolute theory of transposition. It does not, of course, disprove the relative theory with regard to other situations or deny, outright, relational perception to the rat. Many factors undoubtedly enter into discrimination behavior. The performances of rats 13, 14, and 15 show how receptor-orienting acts, notably VTE, may influence transfer. Now, the statement has been made that since the absolute theory "rejects the necessity of any 'comparison' behavior, it implies that *transposition should be equally prominent for animals trained in a successive discrimination situation and for those trained in a simultaneous discrimination situation*" (1, p. 378). But, as the authors of that statement are aware (1, pp. 381–382), in so far as successive and simultaneous discrimination problems favor the learning of different receptor-orienting acts or favor the learning of the same act to different degrees, this implication of identical transfer does not follow from the absolute theory.

The experiment is relevant not only to the relative-absolute issue but also to the issue of whether conditioned response generalization is a function of dimensional similarity, as Spence contends, or of "common elements." A proponent of the latter theory is Wolpe (11), who holds that the amount of generalization depends on the number of "afferent neurones" excited in common by the conditioned and nonconditioned stimuli. Wolpe states explicitly that his theory "would flatly contradict Spence's . . . expectation that if the generalized response to a stimulus close to the conditioned stimulus is extinguished, the generalized response to a stimulus close to the other side of the conditioned stimulus in the same dimension will be found to be stronger than the response to the conditioned stimulus itself" (11, p. 9). It was Spence's expectation which this experiment confirmed while the prediction of the common-element theory was not substantiated.

The experiment's relevance for comparative psychology is more difficult to assess. In a previous study (4), children were trained in size discriminations and their transposition behavior examined. With even prelinguistic *S*s, the results suggested that a relational organization underlay relational transfer. If these results mean that the relative theory holds for children, then it must be asked: why should rats conform to the absolute theory and children to the relative theory? Is the relative mechanism altogether absent in the rat and the absolute mechanism absent in the child? Or, do the two mechanisms coexist in one or both animal forms but manifest themselves under different conditions? Ascent of the phylogenetic scale from rat to man might involve an abrupt change from one mechanism to the other; alternatively, it might involve a change, either gradual or sudden, in the relative importance of the two coexisting mechanisms. Either way, comparative psychology will want to know where those changes take place.

SUMMARY

When applied to rats, the relative and absolute theories of transposition make, under certain conditions, qualitatively different predictions about the transfer behavior of individual animals. The present experiment sought to test the validity of those divergent predictions for each of 15 *S*s trained to discriminate between two circles of different size. Of the 12 rats showing transposition, each behaved in the manner predicted by the absolute theory. The three remaining rats did not show transposition, and in consequence their performances were irrelevant to the immediate theoretical issue.

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NONSPATIAL DELAYED RESPONSE TO TRIAL-UNIQUE STIMULI IN SOPHISTICATED CHIMPANZEES[1]

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A number of investigations (e.g., 5) have indicated that nonspatial delayed response (NSDR) is very difficult for chimpanzees. However, a single pair of visual stimuli has commonly been used throughout an experiment; and since test sessions ordinarily include a large number of massed trials, with frequent changes of stimulus polarity, retroactive inhibition (or interference, or stimulus perseveration) may be added to whatever other factors may operate to depress performance. Since the test is intended to evaluate "immediate visual memory," rather than susceptibility to retroactive inhibition, it would seem desirable to minimize the latter factor. This could be done by wide spacing of trials, or by use of a new pair of stimuli on each trial (trial-unique stimuli). The latter approach was used in the present investigation.

With this procedure, each NSDR trial may be considered analogous to a visual discrimination problem which is run for two trials: a training trial (represented by the NSDR baiting procedure) and a test trial (the choice after delay, in NSDR). Since naive animals (including man) make near-chance scores for the first few discrimination trials, it would be superfluous to test such *S*s on trial-unique NSDR. (Replacement of the first discrimination trial with the NSDR baiting procedure could hardly make for more effective learning; in fact, learning might, conceivably, be retarded by the absence of active participation and/or direct reward.) We have therefore used chimpanzees that were already sophisticated in visual discrimination work and whose second-trial accuracy was well above chance.

Harlow (1) has shown that sophisticated monkeys can do significantly better than chance on trial-unique NSDR, with minimal delays. In the present work, longer delay intervals were included, and spaced-trial discrimination problems were used for comparison.

METHOD

Our apparatus was the same as that used previously in discrimination learning-set work (4). It includes a horizontally sliding tray with two food wells, and a vertically sliding opaque screen.

Our stimuli were drawn from a supply of about six hundred objects constructed of assorted combinations of scrap materials. They differed in form, size, color, and texture. It was necessary to use some of these objects more than once, so they were not strictly trial unique; however, they were rearranged in new pairs for reuse, and were reused only after long intervals, so they were presumably trial unique in effect.

Each NSDR trial involved the following steps:

1. Two new objects were placed over the two food wells in the sliding tray. The position of the correct object varied from trial to trial in a predetermined, irregular order.

2. The opaque screen was raised, and *S* was allowed to see a piece of food being placed under the correct object. (Some *S*s soon became reluctant to watch the baiting. In such cases, *E* waited and coaxed until he was sure that *S* was at least looking toward the apparatus.)

3. The opaque screen was lowered for the duration of the delay interval (from 10 to 60 sec.). In half the trials, the positions of the objects and reward were interchanged during this period; these position-shift trials were mixed with constant-position trials in an irregular, predetermined order independent of that which determined original position.

4. The screen was raised, and the tray was slid forward to permit *S* to displace an object. If it chose incorrectly, the tray was retracted for about 5 sec., then returned to permit correction of the error.

Each *S* was introduced to this procedure by ten transitional trials during which the screen was not lowered, so the *S*s could see the positions of objects and reward being interchanged. These trials are not included in the results.

PRELIMINARY WORK

All preliminary testing was done at the rate of ten trials per session.

Don (17 years old) had acquired a learning set (4) which enabled him to do discrimination problems with 90 per cent second-trial accuracy. He was given ten NSDR trials each, at delays of 10, 15, 25, and 40 sec., followed by 100 trials at 60-sec. delay. His score for these 140 trials was 89 per cent correct. His accuracy

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[1] This research was assisted by a grant from the Samuel S. Fels Fund.

[2] Now at the University of Texas.

remained essentially constant throughout the 14 sessions.

Frans (6 years old) was first tested on NSDR after completion of the first phase of his discrimination set training (4), when his second-trial accuracy was about 82 per cent. He was given ten NSDR trials each, at delays of 10, 20, 40, and 40 sec., and averaged 75 per cent correct. He was then given 60 trials at 60-sec. delay, and averaged 68 per cent correct, with no improvement during this period.

When Frans had completed the second phase of discrimination set training, and reached a second-trial accuracy of 98 per cent, he was again tested on NSDR, with 10-, 30-, and 60-sec. delays mixed, within each session. He was given 80 trials at each of the shorter intervals, and 160 trials at 60 sec. The results are shown as a solid line in Figure 1. The relationship between delay interval and accuracy is not highly significant ($p = .15$). There was no indication of improvement with practice. It was noted that Frans was often reluctant to watch the NSDR baiting.

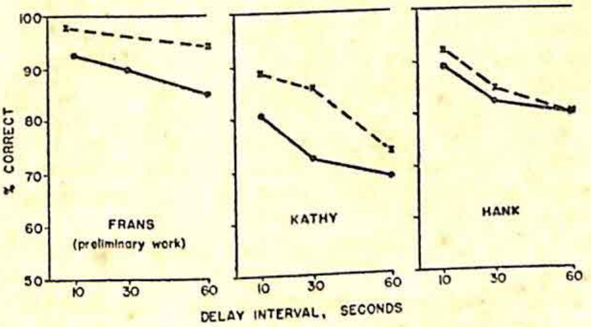

FIG. 1. Forgetting curves for discrimination problems (dashed lines) and trial-unique nonspatial delayed response (solid lines)

Frans's lower accuracy with longer delays suggested a small amount of forgetting during the delay interval. To determine whether such forgetting might also occur after the first trial of a discrimination problem, Frans was next run on 80 two-trial discriminations, with a 60-sec. delay between trials. His second-trial accuracy is shown as a function of intertrial delay by a dashed curve in Figure 1. (The first point on this curve is based on his previous discrimination work [4], where the delay had been minimal—something less than 10 sec.) The relationship between delay interval and accuracy is not statistically significant, but there is a reliable difference between the two procedures, with 60-sec. intervals ($p = .05$).

FINAL EXPERIMENT

Kathy (3 years old) and Hank (7 years old) were tested after completing training on discrimination learning set (4) and concurrent discrimination (3).

Method

Each session consisted of three NSDR trials at each of three delays, 10, 30, and 60 sec., plus three two-trial discrimination problems with each of these delay intervals between trials. Discrimination problems alternated with NSDR trials, and delay intervals were distributed evenly throughout each session. There were thus 27 trials per session, of which 18 (the NSDR trials and discrimination test trials) provided data. Testing was continued until each S had accumulated 600 data trials—100 NSDR trials and 100 discrimination test trials at each of the three delay intervals.

Results

Figure 1 shows accuracy as a function of delay for each S and procedure, individually. When data for the two Ss are pooled, the relationship between accuracy and delay is statistically significant ($p < .05$ for NSDR, and $p < .01$ for discrimination).

Hank's performance was almost identical for the two procedures, but Kathy did significantly better on discrimination than on NSDR ($p = .01$). It was noted that Kathy was often very reluctant to watch the NSDR baiting, while Hank was exceptionally willing to do so.

There was no indication of improvement in performance during the period of testing.

DISCUSSION

Although chimpanzees with learning sets can learn a new problem in one trial, they do not necessarily learn it very well, much less overlearn it. It is not surprising, therefore, that an appreciable amount of forgetting occurs during the next 60 sec., as shown in the broken lines of Figure 1. Harlow and Warren (2) have obtained similar results with monkeys for those problems where the first trial was correct, although, when the first trial was incorrect, second-trial accuracy was independent of the intertrial delay. (We have replotted the discrimination curves of Figure 1, with the second trials segregated according to the correctness of the first trial. There was no appreciable difference between the curves for first trial correct and those for first trial incorrect. This may be related to our use of delayed correction procedure, which makes all trials "correct," in the sense that they end with S's displacing the correct object and obtaining reward.)

Patton, Koskoff, and Miller (6) have reported no influence of intertrial delay on second-trial accuracy; however, their shorter delays were used first and longer ones last, so that practice effect may have obscured the issue.

Our results suggest that trial-unique

NSDR is no more difficult than discrimination learning, provided that *S* perceives the baiting in NSDR. The chimpanzees that were highly attentive to baiting (Don and Hank) displayed essentially the same performance with both procedures. Those that were reluctant to watch the baiting (Frans and Kathy) performed less accurately on NSDR than on discrimination, but showed no appreciable difference in rate of forgetting.

When *S* is required to displace an object on the first trial of a discrimination problem, we may be reasonably confident that it perceives the object and the baited or empty food well beneath it. In NSDR, however, it is quite possible for *S* to look the other way during baiting, and some *S*s do. The *E*'s attempts to attract *S*'s attention to baiting are not always entirely successful, even though *S* does look in the right general direction.

SUMMARY

Four chimpanzees with discrimination learning sets were tested on nonspatial delayed response, using a new pair of stimulus objects on each trial. Three of them were also tested on two-trial discrimination problems, with a delay interval between trials.

Rate of forgetting during the first minute was essentially the same for nonspatial delayed response as for discrimination. Over-all accuracy of performance was also essentially the same for those *S*s that were attentive to baiting.

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